Facilitating forest recovery in Awarua wetland, Southland, New Zealand

A thesis submitted in partial fulfilment of the requirements for the
Degree of
DOCTOR OF PHILOSOPHY
In ECOLOGY

By Olivia Rata Burge
At the University of Canterbury
Christchurch,
New Zealand

Contents

Chapter Three: Monitoring duration and interspecies interference affect detection rates in chew cards

Chapter Four: The folly of charismatic methods: bird perches

Chapter Five: Successional engineering: is *Chionochloa rubra* a suitable nurse species for native forest?

Abstract

In New Zealand, large-scale disturbance in the form of anthropogenic burning and clearance for agriculture began with Maori settlement in 1280 AD and intensified with European settlement after 1840. Successional vegetation in New Zealand is highly flammable when certain native trees (*Leptospermum scoparium*, *Kunzea ericoides*) and invasive species (*Ulex europaeus*) establish. Succession to forest, where abiotic conditions allow it, is slowed by seedling herbivory and reduced dispersal and is dependent on facilitative effects of the early stage canopy trees. The aim of this thesis was to quantify how herbivory, dispersal and facilitation interact to affect regeneration in Awarua wetland near Invercargill, and to test restoration techniques at the site. Drier parts of the Awarua wetland complex were previously in lowland native forest but are now dominated by *L. scoparium* and have been burnt repeatedly.

I tested whether regeneration was dispersal limited using a vegetation survey at four sites in the wetland. I found dispersal limitation at multiple scales (among and within sites). This conclusion was strengthened by seed trapping around a forest remnant, where I found only three of 11 native forest species were being dispersed even small distances (< 150 m) from the remnant.

I quantified the effects of competition, facilitation, and seed predation and herbivory on seedling establishment, survival, growth, and species diversity and evenness with a seed sowing experiment of 2.6 years duration. I found that abiotic conditions in the wetland were generally suitable for forest species to grow; that the *L. scoparium* was relatively young and should allow more forest regeneration as it ages; that the wetland was seed limited; and that excluding herbivory and seed predation doubled the number of surviving seedlings.

Chionochloa tussock communities are naturally present within the wetland and increase in abundance after fire, in the absence of which they are invaded by *L.*

scoparium. I used a seedling and seed sowing experiment to test whether forest seedlings could successfully establish in tussock areas. I found seedling establishment was limited by pH in both tussock and control (*L. scoparium*) areas, and confirmed that biotic constraints (herbivory and seed predation) were slowing regeneration.

I also tested two relatively novel methods in New Zealand. I conducted three pest surveys of the wetland using chew cards and propose guidelines for nationally consistent use that reduce errors due to interference between mammal species. I tested the cost effectiveness of bird perches for speeding succession in restoration ecology, and found they will rarely, if ever, be the best option.

Finally, I assessed factors affecting the speed of forest regeneration at a landscape scale with a spatially explicit vegetation model, parameterised from my field experiments and the literature. This model suggests that the shortage of existing forest fragments is the key factor slowing regeneration within the landscape, and interacts with seed predation and seedling herbivory.

The Ramsar convention on wetlands requires maintaining ecological character in listed wetlands such as Awarua. My results contribute to this planning by highlighting the current vulnerability of the wetland to fire, showing the importance of seed limitation, and quantifying which actions would best facilitate forest regeneration.

Acknowledgements

I am very grateful to my supervisors for generously sharing their time, advice and knowledge with me. Dave, thank you for your support, the freedom to explore all manner of side projects, and your advice on topics ranging from seed trapping to successional theory. Janet, thank you for your constructive feedback, facilitating my access to LandCare equipment, facilities and interns, and most especially for your support throughout the thesis. George, thank you for welcoming me in Auckland, providing indispensable advice and help with NetLogo, the Awarua spatial model, and Chapter 6.

I have had the privilege of working with Department of Conservation staff in the Christchurch and Invercargill offices. I owe a huge debt of gratitude to all those who went above the call of duty: Lynne Huggins, Brian Rance, Polly Bulling, Sarah Crump, Colin Bishop, and Sarah Thorne for facilitating and supporting my project in Invercargill, and Hugh Robertson and Mary Beech in Christchurch. Last, but certainly not least, George Ledgard, whose vision and work catalyzed the project in the first place, and assistance with fieldwork.

Awarua is not the easiest place to get around in, nor subject to the most temperate weather. Therefore a warm thank you to Michelle Wiedner and Mark Stoop for arriving in the dark and then spending a week assisting with a vegetation survey, gorse and all; Blair Lawrence for helping me count seedlings in the snow; Rachel Harley for our fieldwork exchange, of which I think I got the nicer experience; Carol Frost for our escapade in Kaikoura hunting down recalcitrant seed traps, and between-conference jaunt in Sweden; Anna for indomitable spirit as we killed > 300 seedlings in the name of science; Roma Babington for providing the full range of accommodation, footballing opportunities and best quality moral support while down south; and to Anna and Sophie Hale for assistance in the lab.

Thank you also to Matt McGlone, for career advice; Sarah Richardson, for stats advice; Matt Walters, for sharing his immense knowledge on science communication; Kim Roberts for help organising lab and field work gear; the terrestrial ecology lab group (particularly Laura, Jane, Josh, Kevin, Lauretta, Marine & Archie); and the brilliant Jenny Ladley.

I'm the last of a quadruplet of post-graduate students in my office to finish. Rachel, Sarah and Charlotte, thank you for adopting the non-physiologist. I will miss our camaraderie, team problem solving and support which went beyond the confines of the officeFort, but long may it continue from afar.

I would like to acknowledge the financial support of the Department of Conservation, through the Awarai-Kākāriki programme, and the Miss E L Hellaby Indigenous Grasslands Research Trust, without which this thesis would have been impossible. Additional funding and support in kind was provided by LandCare Research, New Zealand eScience Infrastructure, the New Zealand Wetland Trust, and the Ngāi Tahu Research Centre, for which I am very grateful.

I am very grateful to my friends for their support, friendship, and patience during this thesis. A huge thank you to Tim, for your support, encouragement, hydrational encouragement, advice, and care.

Finally, to my parents, brother, and family, thank you.

Chapter One: Restoration ecology & Awarua wetland

1.1 Restoration ecology

Restoration ecology has been termed 'ecological architecture': a mix of sociology, art, and science (Davis & Slobodkin 2004). It has been more formally defined by the Society for Restoration Ecology as '*the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed*' (SER [Society for Ecological Restoration International Science & Policy Working Group] 2004). The question of what state to restore to is a value-based question (Diamond 1987), with the reference, or desired state, often one that has occurred in the past (SER 2004). Once the reference state has been decided, the next question is whether active intervention will be required to assist natural regeneration. Natural forest regeneration is the process by which a disturbed site is colonised by shrubs and trees. 'Passive restoration' does not involve assisting natural forest regeneration by supplementary actions, but can include the cessation of on-going practices that inhibit natural regeneration, such as grazing (Melo *et al.* 2013) or controlling fire on the site (Janzen 2002). 'Active restoration' involves some form of plant addition, including enrichment planting, direct seeding, applied nucleation and agroforestry (Benayas, Bullock & Newton 2008).

Natural regeneration may be prevented by self-perpetuating novel ecosystems (Norton 2009) or slowed by seed limitation, a lack of dispersers, or unsuitable abiotic conditions (Benayas, Bullock & Newton 2008). Although passive restoration is generally less expensive than active restoration (Zahawi, Reid & Holl 2014), successful passive restoration will not necessarily be inexpensive, nor avoid the need for on-going active management of the site. Fire management (Janzen 2002), stock incursion (Birch *et al.* 2010) and control of pest species (Vitousek *et al.* 1997) are all costly and require continued management;

however, the relative biodiversity value of sites may be dependent upon such strategies (Dymond, Ausseil & Overton 2008).

If the natural rate of regeneration is considered to be slow, restoration actions will be most effective if they address the rate-limiting step. In their review paper, Suding, Gross & Houseman (2004) note that species' invasions, loss of landscape connectivity and loss of native seed sources, and the interaction of these factors with the physical environment, are the key influences of restoration success. Identifying relevant requires site-specific investigations to avoid 'bottlenecks' in the process of succession (MacMahon 1987), of which many are possible (Figure 1.1).

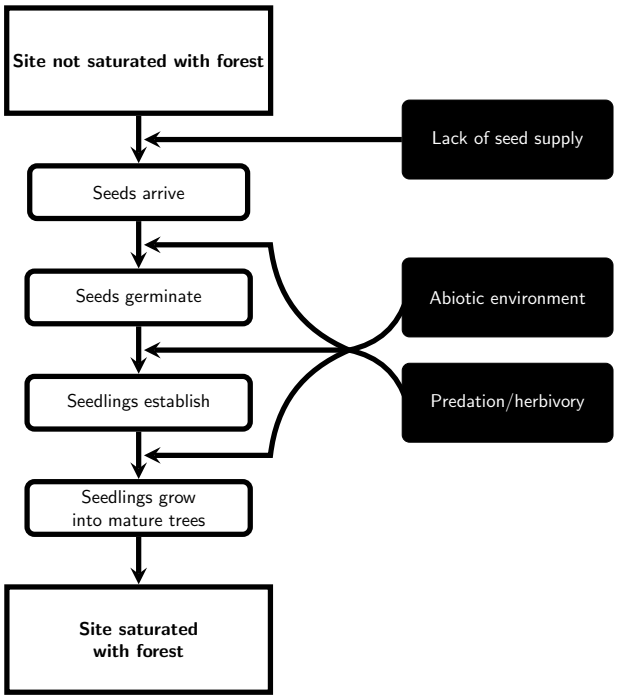


Figure 1.1: The regeneration process (white boxes) and relevant constraints (black boxes). Some constraints may be influenced by several variables. For example, lack of seed supply may be due to lack of seed sources, or a lack of delivered seeds due to inadequate dispersal. Constraints may be absolute (filtering effects so strong no individuals reach the next stage), or relative (the proportion of individuals making it through to the next stage is reduced proportionate to the strength of the constraint).

1.2 Wetland & forest conservation status New Zealand

Wetlands are the interface between land and water (Johnson & Gerbeaux 2004): areas with water-saturated soils or that are covered with shallow water (McGlone 2009). New Zealand is estimated to have once had 10% (2.47 million

ha) of its mainland landmass in wetlands. Ten percent of the historical wetland extent (249,776 ha) remain (Ausseil *et al.* 2008) although as McGlone (2009) points out, wetlands vary enormously in biological and physical characteristics. In a review of wetland protection in New Zealand, Robertson (2016) notes that there are substantial biogeographical biases in areas under protection – wetland types differ across regions in the proportion of area protected both in relation to current and historic wetland extent. Where wetlands lie on private land, restrictions on their use and the clearance of indigenous forest are imposed by the Resource Management Act 1991, which seeks to preserve the natural character of wetlands (Section 6(a)) and protect areas of significant vegetation (Section 6(c)) as national priorities. Subordinate planning documents, such as regional and district plans, also regulate land use on private land.

Less than 1000 years ago, 85-90% of New Zealand was forested (McGlone 1989; Perry, Wilmshurst & McGlone 2014). The arrival of Polynesian settlers led to rapid deforestation (McWethy *et al.* 2010; Perry *et al.* 2012), and by the time of European arrival in the early 1800s, forest cover had been reduced to 68% of the land area (Salmon 1975; McGlone 1983). Forest cover has since been reduced to 24% of mainland New Zealand (Ewers *et al.* 2006).

Southland, the most southern region of mainland New Zealand, contains the second-greatest proportion of national wetland extent, but has lost a disproportionate amount compared to historic estimates of cover (Figure 1.2). There are 32,970 ha of wetland remaining, which is estimated to be 7.9% of the historic wetland extent within the region. The Southland region is estimated to have had 76% forest cover in pre-human times; it now contains 36% (Ausseil *et al.* 2008). This is more than the national average, but remaining forest is in national parks in the Catlins (to the east) and Fiordland (to the west), with relatively much less lowland forest left on the Southland plains.

1.3 Awarua wetland

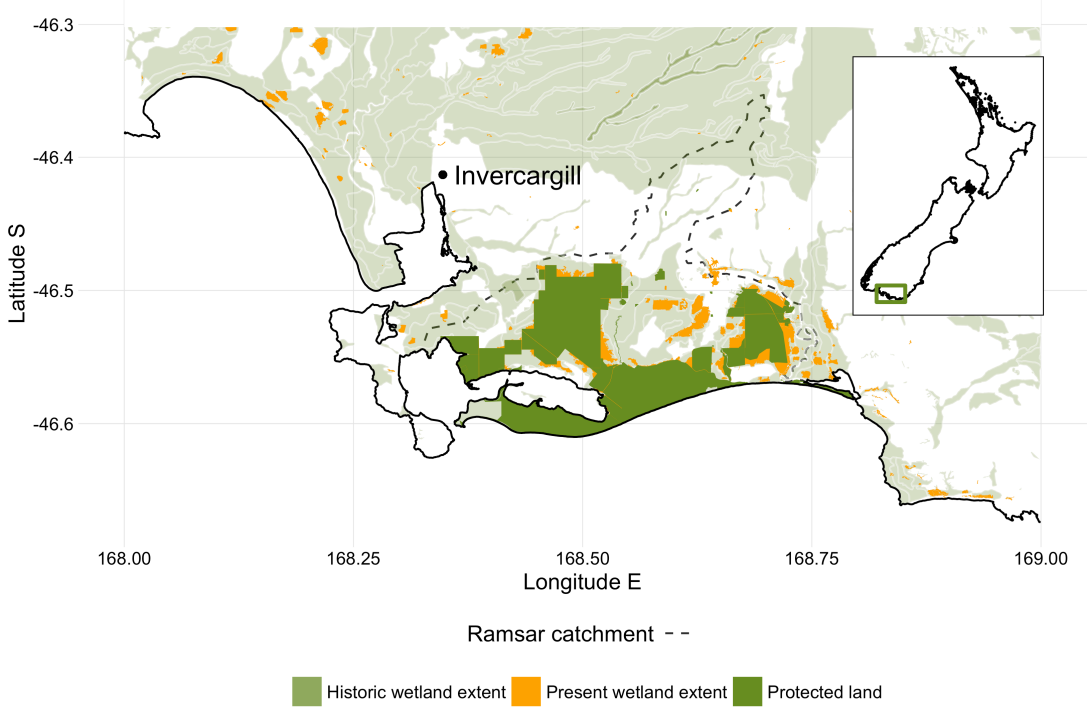


Figure 1.2: Awarua wetland, and inset, the catchment's location in New Zealand. The dashed line demarcates the watershed catchment of Awarua wetland (source: Department of Conservation), initially defined for researching landuse contributing to nutrient inputs to Waituna Lagoon, which forms part of the protected wetland area, and the listed Ramsar area. The dark green indicates land that is currently protected – either private land under conservation covenants or public conservation land. The orange indicates current wetland extent (data layer provided by Department of Conservation; dataset compiled as described in Ausseil *et al.* (2008)). The light green indicates land considered to have been wetland historically (data layer provided by Department of Conservation; cover was estimated from soil information held in the New Zealand Land Resource Inventory (NZLRI) database).

At 20,000 ha, Awarua is New Zealand's largest wetland complex (Figure 1.2). Despite its size, a recent study of the relative importance of wetland sites within biogeographic regions (Ausseil *et al.* 2008) found that due to its lower ecological integrity (of 0.41), Awarua ranked of 'lower importance' than Fiordland's Grebe wetland (ecological integrity of 0.95; 312 ha, located in Fiordland national park). The majority of the terrestrial areas of Awarua wetland (>10,000 ha) are covered in mānuka (*Leptospermum scoparium*), an early-successional native tree species (Anon. 2010). The most common land use surrounding the wetland is intensive agriculture (Figure 1.3).

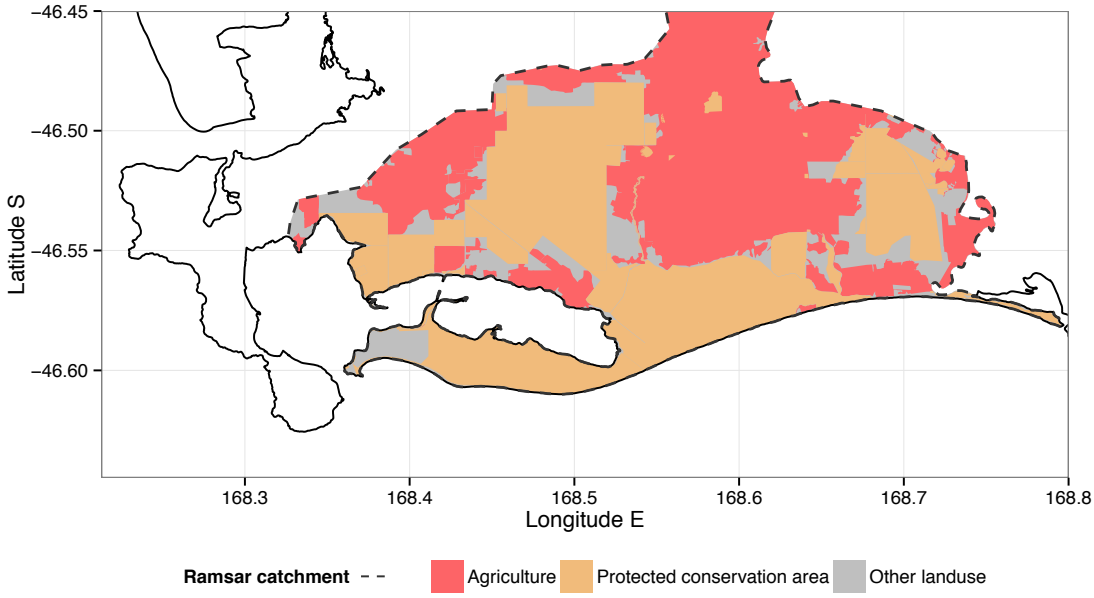


Figure 1.3: Land use within the Awarua wetland catchment (delimited by dashed line) Southland, New Zealand. The tan indicates protected areas (not necessarily contiguous with Ramsar extent [see section 1.4], and including small QEII conservation covenants in the centre). 'Other landuse' areas are undeveloped privately owned land, industrial areas, exotic forestry or roads.

The use of fire is regulated by the local fire authority, however the wetland has been subject to multiple anthropogenic fires (Southland Regional Fire Authority 2015). The last three fires (January 2009, October 2009 and November 2012) burnt an estimated 2029 ha of wetland, and cost in excess of NZ$90,000 in fire control (Figure 1.4).

Fires in the wetland kill mid- and late-successional vegetation, leaving burnt areas to regenerate with grass and tussock species, mānuka, and invasive shrub species (Johnson 2001). The dominance of mānuka in terrestrial areas is considered to have been induced by anthropogenic disturbance (Johnson 2001); in pollen cores taken within the wetland the increase in early-successional species and mānuka correlates with increased charcoal following Maori and European settlement (Wilmshurst J, 2015, pers. comm.), where previously large trees dominated. Given the extent of agriculture, fragmented seed sources for

forest species and relatively common large anthropogenic fires, a key question for the management of the wetland is whether, in the absence of intervention, it is on a trajectory to an 'acceptable' state. There is no official desired reference state for the wetland; the vision for Awarua is 'to protect a large coastal low-lying plain of bogs, swamps, heaths, forests and open water' (Robertson & Suggate 2011, p 10). Altered hydrological regimes caused by drainage and forest clearance might make natural regeneration to the mosaic of forest that historically existed impossible, however, a slow return to forest would likely be more desirable than the system becoming dominated by invasive shrub species and early-successional vegetation, both of which reinforce the frequency and extent of fire within the wetlands (Perry *et al.* 2015). Dominance by invasive shrubs may also be associated with reduced biodiversity and aesthetic values associated with the wetland.

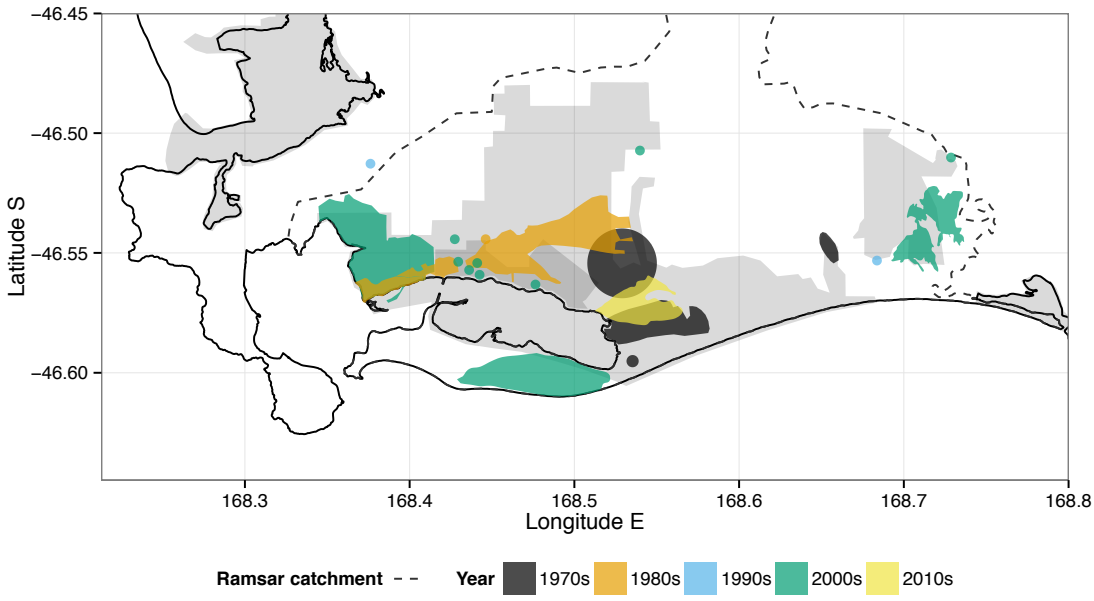


Figure 1.4: Fire history within the wider Awarua catchment, Southland, New Zealand. Shaded grey areas are the areas designated as the "Awarua wetlands" site recognised under the Ramsar convention. Polygons indicate extent of fire (approximate indication only for early fires in the 1970s). The dashed line delimits the catchment for Awarua wetland. Fire data sourced from Southland Rural Fire Authority, all other data from the Department of Conservation.

1.4 Ecological character and the Ramsar convention

The Convention on Wetlands of International Importance (usually referred to as the Ramsar convention) was adopted in the city of Ramsar, Iran in 1971. The intergovernmental treaty is aimed at the conservation and wise use of wetlands. Article 2.4 of the Ramsar convention requires countries that adopt it to list at least one qualifying wetland in the List of Wetlands of International Importance. Wetlands on the list are recognised as being of international and national importance.

New Zealand adopted the convention in 1976 and currently has six wetlands listed, covering 55,512 ha in total. By adopting the convention, New Zealand has made a commitment to formulate and implement planning to promote the conservation of listed wetlands (Article 3.1). Where there is a change (or likely change, or change in progress) in the ecological character of any listed wetland due to technological developments, pollution or other human interference (Article 3.2) this must be communicated to the secretariat of the convention (currently the IUCN, Article 8). The Strategic Plan (adopted by the 12th Meeting of the Conference of the Parties, Punta del Este, Uruguay, 1-9 June 2015) includes the following targets: restoring or maintaining the ecological character of Ramsar sites; addressing threats to sites that are at risk of ecological character change; and initiating restoration of degraded wetlands.

Awarua wetland was the first wetland to be designated under Ramsar by New Zealand (13 August 1976), with 3,500 ha included. It was expanded in 2008 to its present extent of 20,000 ha. The wetland met several criteria for Ramsar convention inclusion: it includes species more commonly found in alpine ecosystems; it provides habitat for migratory (internal and international) wading birds, and threatened species, including endemic Galaxiid species; and the diversity of bird life (81 species found). The Ramsar-recognised areas of the site include a lagoon (Waituna Lagoon), shallow water estuaries (Awarua Bay, Toetoes Harbour and New River Estuary), and a large blanket peat bog. The terrestrial peat bog area is the area in which fieldwork for this PhD took place.

Awarua is also included in a national programme ("Awarai Kākāriki", in English, Green Waterway) that is aimed at reducing knowledge gaps which currently limit the conservation of New Zealand's wetland ecosytems. Existing work has been undertaken by the Department of Conservation at the site to fence areas of the wetland to exclude stock; purchase land for restoration (250 ha bought, 5 ha restored); control weeds and pest species (black back gulls [*Larus dominicanus*] and deer) and decrease the nutrient inputs to Waituna Lagoon (Robertson & Suggate 2011). Ongoing threats identified by the Awarai-Kākāriki programme, together with a regional council report on local land use change, include fire, weeds, and ongoing loss of wetlands on private land to agricultural intensification (Robertson & Suggate 2011; Ledgard 2013). This thesis sought to investigate the different trajectories in the condition of terrestrial areas of Awarua, and in particular, to identify constraints to restoration of the desired state (in this case, forest). Further, where multiple constraints were identified, this thesis prioritise those that should be addressed first.

1.5 Thesis outline

The main objectives of this thesis were to identify and quantify constraints to native forest regeneration in Awarua wetland, and to test potential restoration strategies. The key questions addressed in this thesis are:

1. Whether forest regeneration in the wetland was dispersal or seed limited (Chapter 2);
2. Whether forest species could establish in areas of low regeneration in the wetland, and whether establishment and survival could be increased by preventing seed predation and seedling herbivory, or by clearing competing understorey species (Chapter 2);
3. Which pest mammal species were present in the wetland, and whether pest density decline from edges, meaning pest control was unnecessary in the wetland interior (Chapter 3);
4. The utility of using chew cards, a relatively novel pest monitoring method, for multispecies monitoring (Chapter 3);

5. Whether artificial bird perches can be a financially viable method to increase forest regeneration (Chapter 4);
6. Whether red tussock (*Chionchloa rubra*), a native tussock species that is probably more abundant than historical levels due to its ephemeral establishment after disturbance, could provide a suitable environment for forest seeds and seedlings to be sown and planted into (Chapter 5);
7. What the potential trajectories of wetland succession are at a landscape scale. I combined my experimental results in the preceding chapters with existing GIS information and information from the literature to create a spatially explicit model of regeneration within the Awarua catchment (Chapter 6).
8. Taking into account the work in preceding chapters, is the wetland currently in an alternative stable state or stalled succession (Chapter 7) and implications of this discussion for management of the wetland under the Ramsar convention.

Chapter Two: Current constraints on forest regeneration within Awarua-Waituna wetland

2.1 Introduction

Regeneration after large-scale disturbance depends on site-specific factors, landscape-level factors, and processes. The most fundamental factor is species arrival, which is reliant on seed sources existing within the landscape, if not already present at the site, and sufficient dispersal such that seeds arrive at the site. Site-specific factors include abiotic variables – the physical and chemical suitability of the soil (Tilman 1982; Reynolds *et al.* 2003) and environmental stressors such as drought and fire. Site-specific biotic factors affecting regeneration include the composition and degree of primary succession and its facilitative or competitive effect on forest seeds and seedlings (e.g. Holmgren, Scheffer and Huston (1997); Callaway and Walker (1997), see also Chapter 5); and seed predation and seedling herbivory (Janzen 1971; Myster 2004; de Souza Gomes Guarino & Scariot 2014). These constraints can be thought of either as a series of filters through which individual organisms must pass (Holl 1999; Fattorini & Halle 2004); or as a 'niche'. The potential niche may be considered a subset of the fundamental niche (Hutchinson 1978), as the sum of all areas *that actually exist* in which a species' intrinsic requirements and the characteristics of the environment would allow it to establish (Jackson & Overpeck 2000); while the realised niche is the subset of the potential niche that is suitable for species after accounting for competition, predation and herbivory (Pulliam 2000), but also expanded by facilitation (Bulleri *et al.* 2015).

In this chapter I test the strength of the filters discussed below in relation to seed dispersal and arrival, seed germination and seedling survival.

"Dispersal limitation" can be defined as a "recruitment limitation resulting from the failure of seeds to arrive at favourable sites"; while "recruitment limitation" can be defined as "the failure of a species to establish in all sites that are favourable to its growth and survival" (Wang & Smith, 2002, p 8). Therefore dispersal limitation can be regarded as a subset of recruitment limitation, but the two are not equivalents. Dispersal is a commonly cited constraint of species distributions (Brown, Stevens & Kaufman 1996; Gaston 1996); however Lester *et al.* (2007) conclude that although dispersal can be an important determinant of range size, other processes should be considered as well. Perhaps the most well-known inclusive treatment of the determinants of range size is Grubb (1977), in which the factors affecting whether a gap will be successfully colonised by a given plant species are discussed as including the time of gap formation and its size and shape; whether the plant's dispersal in time and space allow it to reach the gap when it is empty; and whether the gap is suitable for germination, establishment and survival in terms of biotic and abiotic factors. Beyond initial colonisation as a seed and then germinant, Grubb (1977) notes that conditions which favour establishment may not be those which favour germination.

Forest regeneration in New Zealand

New Zealand forest is vulnerable to interrupted succession due to the high proportion of endozoochorus (primarily bird-dispersed) species (although estimates range from 70% of tree species - Burrows (1994) to 59% of New Zealand tree species being 'fleshy-fruited' – Kelly et al (2010)) and the recent reductions in the dispersing frugivorous bird species and populations (Holdaway, Worthy & Tennyson 2001); its relative lack of a persistent seed bank to buffer interruptions to bird dispersal (Burrows 1994; Bray, Burke & Struik 1999); invasive plant species which may displace or outcompete native species; and invasive mammal species, some of which prey upon native bird, lizard and invertebrate species, some of which eat native seeds or native seedlings, and some who do both (Clout 2001). Both herbivory by exotic species on natives and facilitative exotic species have been shown to change the trajectory of native

forest succession (Allen, Payton & Knowlton 1984; Allen, Lee & Rance 1994; Cowan *et al.* 1997; Wardle *et al.* 2001; Wilson *et al.* 2006; Sullivan, Williams & Timmins 2007). Fires have increased since human settlement of New Zealand (Wilmshurst 1997; Wilmshurst, Eden & Froggatt 1999), with a resulting destructive effect on forest cover and regeneration (McWethy *et al.* 2010; Perry, Wilmshurst & McGlone 2014).

Kānuka (*Kunzea ericoides*, retaining the classification of Webb *et al.* (1988)) and mānuka (*Leptospermum scoparium*), along with *Pteridium esculentum* (Leathwick & Rogers 1996*,* were common in early phases of vegetation succession prior to European settlement, with a transition to taller, broad-leaved species around 100 years post-disturbance (Williams & Karl 2002). This is longer than the 30-year transition expected when gorse – an invasive weedy species – is the nurse crop in some areas, such as Nelson, in the north of the South Island, New Zealand (Williams & Karl 2002). At present, mānuka and kānuka often form dominant components of early-successional vegetation communities following disturbance or abandonment of agricultural land (Coomes *et al.* 2003), but may be replaced by invasive shrub species (Perry *et al.* 2010). Allen *et al.* (1992) observed a marked rise in frequency of native forest species in kānuka study plots from 50 years corresponding with a substantial decrease in the stem density of the kānuka. Decrease in the stem density of mānuka or kānuka due to self-thinning is often accompanied by an opening of the canopy, allowing sufficient light for regeneration of forest species. Allen *et al.* (1992) note that it is the decline in kānuka that allows the establishment of later successional species, rather than the presence of kānuka. However, to the extent that a canopy species is required to inhibit the establishment of a grassy sward which would otherwise prevent later succession, the presence of a nurse species such as mānuka or kānuka is required. Smale, Hall and Gardner (1995) note that exclusion of herbivorous deer from kānuka and mānuka increased the establishment of early-stage forest species (in this case, the broad-leaved small tree species *Melicytus ramiflorus* and *Myrsine australis*), 10 years post-exclusion. Richardson, Holdaway and Carswell (2014) found evidence of a stalled

succession under mānuka and kānuka in forests in Te Urewera, New Zealand, which was considered most likely due to seed predation and seedling herbivory.

Mānuka is considered to facilitate forest regeneration by creating a less stressful environment (protection from excessive sunshine and environmental extremes; suppression of weeds) (Esler & Astridge 1974; Ogden & Stewart 1995; Stephens, Molan & Clarkson 2005). Estimates of the age at which it is likely to be overtopped by other forest trees vary; however mānuka is not known to self-perpetuate, except where broadleaved forest is prevented or abiotic conditions are unsuitable for forest (Dobson 1979; Wardle 1991). Mānuka can germinate in low light conditions (Herron, Clemens & Greer 2000), but seedling establishment is low, and establishment is highest in open areas of low, open cover (Grant 1967). Therefore sites containing large areas of mānuka are at risk of being invaded by exotic species, if the process of forest succession is interrupted. Mānuka is capable of having an adverse effect on the likelihood of site-level forest regeneration when the fire return rate is high, due to its flammability (Esler & Astridge 1974). Both mānuka and bracken (*Pteridium esculentum*) are fire-adapted species (Perry, Wilmshurst & McGlone 2014). In boggy and acidic areas within wetland ecosystems, there is a natural environmental niche of mānuka in which forest is unlikely to invade due to abiotic conditions (Burrows 1973).

Awarua wetland is a large (20,000 ha) protected area in Southland, New Zealand. It has been subject to widespread and repeated anthropogenic disturbance in the form of fire and vegetation clearance. Over 10,000 ha of the wetland has been mapped as mānuka-dominated ecosystems, and most of it is thought to have been in a mosaic of podocarp-broadleaf forest prior to disturbance (Johnson 2001). Invasive pest animal species are present in the wetland (see Chapter 3), and domestic animals graze in wetland areas on private land. It is recognised under the Ramsar Convention (1971) as being an internationally significant wetland, and worthy of protection as such. The surrounding catchment is primarily in agriculture, with limited forest seed sources. The frugivorous bird population is unquantified, although the largest extant frugivorous bird in New

Zealand, *Hemiphaga novaeseelandiae* (kereru) have been documented as present in the region (Powlesland, Moran & Wotton 2011).

When to actively manage forest regeneration?

New Zealand has a substantial area of conservation estate (8.5 million hectares DOC (2014)) and insufficient resources to actively manage it all. Only 10% of species at risk of extinction are actively managed; invasive mammalian species are only subject to control on one-eighth of the conservation estate (Wright 2011).

Conservation management ranges from passive to active. Management inputs to protected areas range from 'paper parks' (parks recognised in legislation only, *sensu* Rodríguez and Rodríguez-Clark (2001)), to restoration programmes, aimed at changing a system's state to a more desired one (Aaron *et al.* 2001; Rodríguez & Rodríguez-Clark 2001; Hobbs & Cramer 2008). It is recognised that 'desired states' are a social construct and that the paleoecological record indicates that sites may be capable of various different 'natural' states depending on temporal and environmental changes (La Voie, Zimmermann & Pellerin 2001; Burney & Burney 2007; Willard & Cronin 2007). The necessity for active management of a system depends on how far away it is from a desired state and the likelihood of passive regeneration (Hobbs *et al.* 2011; Holl & Aide 2011). When active management is required, the magnitude of intervention and the desired speed of transition will affect the cost and scale of management required (Holl & Aide 2011). Forest regeneration may occur naturally, or require active restoration efforts.

The primary aim of this chapter is to evaluate the process of regeneration in Awarua-Waituna, given the spatial and temporal context of disturbance, and to determine whether any intervention is required. If intervention is required, I seek to determine which constraint would be most effective to address. Specifically, I examined:

1. Is native forest regeneration within the wetland seed-source or dispersal-limited? If so, at what scale?
2. If native seeds of forest species reach the wetland:
    a. To what extent will the existing abiotic environment limit regeneration?
    b. To what extent will the existing biotic environment limit regeneration, through seed predation, herbivory and competition?
3. Does the current age of the mānuka and presence of exotic plant and animal species within the wetland pose a risk to succession such that management intervention is necessary to ensure native forest regeneration?

2.2 Methods

The research questions were addressed using three complementary experiments ("vegetation survey", "seed sowing experiment", "seed trapping experiment"), which are summarised in Table 2.1. The experiments will be described separately as the vegetation survey and seed sowing experiment relate to multiple research questions, but are synthesised in the Discussion.

Table 2.1: Relationship between research questions and the vegetation survey, seed sowing experiment and seed trapping experiments

Research question	Experiment	Treatment or explanatory variable	Response
Is native forest regeneration within the wetland seed-source or dispersal-limited?	Vegetation survey	Site and plot-level distance from native seed source	Presence or absence and amount of regeneration
	Seed traps	Distance from native seed source	Number and species of native seeds found
	Seed sowing	+/- seeds sown	Seed germination, seedling establishment
To what extent will the existing biotic environment limit regeneration?	Seed sowing	Herbivory and seed predation +/- protection	Seedling survival, biomass (total seedling height in cm), species richness and diversity
	Seed sowing	Facilitation – two natural mānuka canopy types & experimentally thinned type	Seedling survival and biomass
	Seed sowing	Competition +/- understorey clearance	Seedling survival and biomass
To what extent will the existing abiotic environment limit regeneration, through seed predation, herbivory and competition?	Vegetation survey	Abiotic variables (e.g. soil moisture, pH)	Presence or absence and amount of regeneration (number of seedlings and total plot height in cm)
	Seed sowing	Abiotic variables (e.g. soil moisture, pH)	Seedling survival and biomass
Does the current density of the mānuka and presence of exotic plant and animal species within the wetland pose a risk to succession such that management intervention is necessary to ensure native forest regeneration?	Vegetation survey	N/A	Age of mānuka, presence of invasive species

Vegetation survey

Four sites were chosen within Awarua wetland based on access considerations and distance to seed source: Tiwai, Clearwater, Lawsons Rd and Craws Creek (Figure 2.1).

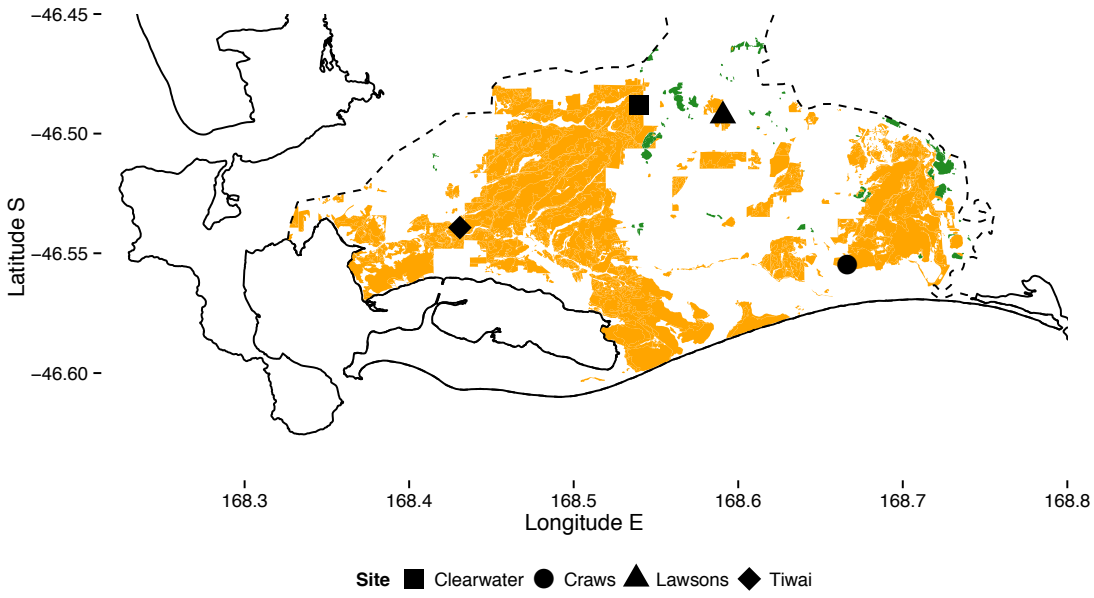


Figure 2.1: Location of vegetation survey sites in Awarua wetland, Southland, New Zealand. Dashed line delineates the catchment of the Ramsar wetland. Orange areas are mānuka; green is late successional native forest. The podocarp-broadleaf forest remnant at Craws Creek is too small to be seen under the site marker.

Tiwai contained the least regeneration, was the western-most survey site and was the farthest from forest remnants (2.4 km away from a small QEII covenanted forest remnant). Clearwater had some regeneration and was moderately far from forest fragments (950 m, across farmland/roads). Lawsons Rd was a privately owned site, some of which had been cleared, and some of which was subject to grazing. It was immediately adjacent to a covenanted site (separate ownership) which contained a small forest remnant and a regenerating forest (350 m from nearest seed source). Craws Creek included a forest remnant (Figure 2.2) and the surrounding mānuka was seen as a 'model' site for forest regeneration under mānuka.

The vegetation survey was conducted over 11 days of fine weather (5, 8 March 2012 and 12 – 20 April 2012). I selected 40 randomly located plots at each site using ArcGIS within the area mapped as mānuka. A minimum separation distance of 20 metres was specified between each plot, and from the site perimeter. Plots were located using GPS. Where plots were found not to be under a mānuka canopy (e.g. in open areas) I chose the closest area under a mānuka canopy. Plots were 2 x 2 m, measured and marked using flagging tape.

Clarkson *et al.* (2004) suggests that a plot of 2 x 2 m is useful as it satisfies the minimal sample areas for relatively short vegetation. It is noted that that 4 m^2 may not adequately represent the community species composition, and minimal area and/or running mean methods may need to be implemented to determine a more appropriate sample size. Conversely, Messaoud and Houle (2006) note that several studies in forest ecosystems have shown how abiotic factors vary in space, at the scale of several metres or even centimetres, meaning plots should be small enough to minimise within-plot heterogeneity. Given the heterogeneity in regeneration over small spatial scales within the wetland observed during site selection, the smaller plot size provided by 2 x 2 m was preferable to a larger plot size that might dilute distinguishing characteristics of regeneration where it occurs.

Within each plot, I first recorded the cover of all non-herbaceous plant species (species list in Appendix 2.1). I recorded the cover of all woody species, including non-natives, which might compete with native forest species as part of the vegetation survey. I then recorded the number and heights of only native later successional woody forest species. I decided before conducting the survey to include *Coprosma foetidissima* if and where it occurred, as it has larger fruits than other *Coprosma* species (Lee, Wilson & Johnson 1988) that might attract frugivores in the absence of other later successional forest species. Other later successional species found were *Carpodetus serratus, Elaeocarpus hookerianus, Griselinia littoralis, Phyllocladus alpinus, Pittosporum tenuifolium, Podocarpus cunninghamii, Pseudopanax crassifolius* and *Raukaua simplex* and hereafter these

nine species (including *C. foetidissima*) will be referred to as "forest species" in the context of this experiment.

After recording the species information I measured variables relating to the abiotic environment and canopy height (which always included some mānuka). Canopy openness was measured using hemispherical photography. Digital Hemispherical Photography (DHP) is recognised as being one of the most accurate and robust techniques available to assess canopy transmittance and understorey light availability (Sharma *et al.* 2012). The camera was placed in the centre of each plot and measured to be 1 m off the ground, orientated to face north and then rotated until level using a spirit level. Photographs were taken so far as possible in light conditions as described in Chan *et al.* (1986). Photographs were analysed using "Gap Light Analyser" software, adjusting the parameters as appropriate (Frazer, Canham & Lertzman 1999). Soil moisture (%) and soil conductivity (mV) were measured using a Delta-T soil moisture meter, which measures soil moisture content by responding to changes in the apparent dielectric constant of moist soil. Depth to groundwater was measured by digging until groundwater was reached, left to reach equilibrium (on average, 15 minutes) and then depth from the soil surface to water surface was measured. Canopy height was measured in the centre of the plot from the ground to the highest point in the canopy using a tape measure.

Distance to forest fragment for sites Tiwai, Clearwater and Lawsons was measured from the centre of each site to the nearest remnant of indigenous later-successional forest, using ArcMap. Craws Creek contained a forest remnant, and so distance from each vegetation survey plot to forest remnant within the Craws Creek site was measured using the SP package (Bivand, Pebesma & Gomez-Rubio 2005) in R (R Core Team 2015), using the GPS point locations of the sites and a point delineating the centre of the remnant (Figure 2.2).

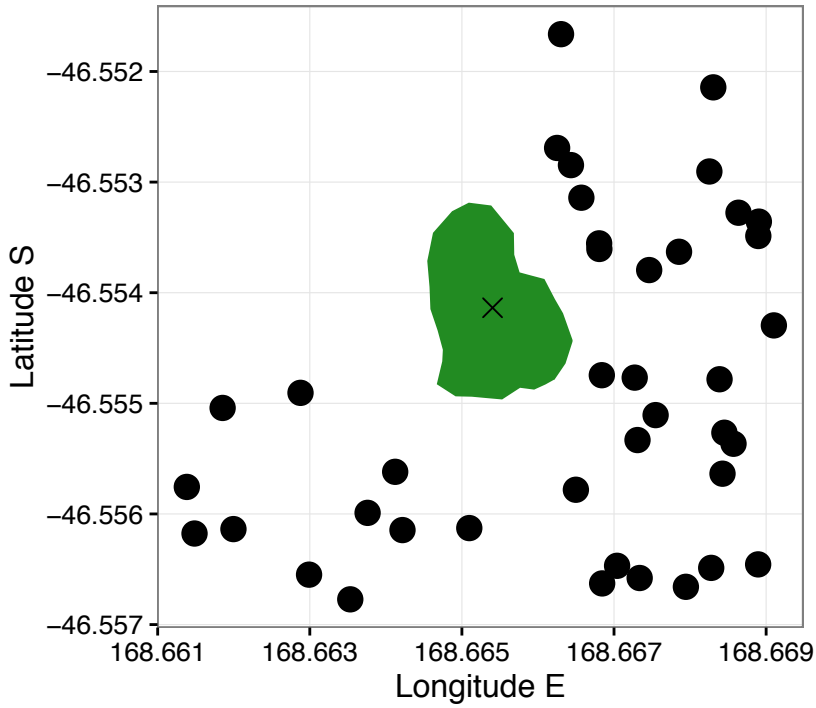


Figure 2.2: Location of plots in Craws Creek. Extent of forest remnant indicated by green polygon, with black cross in centre indicating the point from which distance to remnant centre was measured.

All statistical analyses in this chapter were undertaken with R version 3.2.2 (R Core Team 2015).

I tested whether distance to seed source correlated with the presence of regeneration at the between-site and within-site scale. I tested the between-site correlation by analysing the proportion of plots with forest regeneration using a generalised linear model with a binomial distribution, with site as the predictor variable. I quantified the importance of distance to seed source, abiotic variables and biotic variables (variables relating to the mānuka canopy) to two response variables: the number of forest species seedlings within each plot, and an index of biomass (total height of forest species seedlings, hereafter 'biomass') in each plot, using a boosted regression tree (package DISMO by Hijmans *et al.* (2013) in R). Boosted regression trees draw from both machine learning and traditional

statistical methods. Unlike traditional regression methods that produce one 'best' model, boosted regression trees combine numerous simple tree models to optimise performance. The 'boosting' element of the name comes from the algorithm that builds and combines the collection of models, while 'regression tree' comes from the regression trees (or 'decision trees') that collectively form the group of models combined by boosting (Elith, Leathwick & Hastie 2008). I used a Poisson distribution for seedling counts and a Gaussian distribution for biomass (total seedling and tree height in plot).

I used the resulting model to predict the total biomass at other sites retaining each plots' abiotic variables but under the assumption they were as close to seed source as the range at the Craws Creek site, using the first 400 iterations of trees in the boosting sequence. I checked whether the total abiotic range of each site overlapped with that of Craws Creek using nonmetric multidimensional scaling (NMDS) with Euclidean distance using R package VEGAN (Oksanen *et al.* 2013). The environmental data were on very different scales (depth to groundwater ranged from 15 – 55, conductivity ranged from 275 – 1200, canopy height ranged from 1.55 to 6.40) so data were column-wise (or species-wise, in classic ordination terminology) hellinger-transformed prior to ordination. I used the abiotic variable scores (or species' scores) for the arrows in the ordination diagram and calculated the hull (total area) of each group in R.

I tested which species differed across sites using a multivariate generalised linear model, which provides adjusted p-values for multiple testing (package MVABUND (Wang *et al.* 2014)). I used site as the predictor and percent cover as the response, with a negative binomial distribution.

Seed trapping experiment

I measured seed fall within the broadleaf-podocarp forest remnant at the Craws Creek site (Figure 2.2) and within the mānuka surrounding it. I set up seed trap transects in February 2014 within the forest remnant and at increasing distances (30, 100, and 200 m) from the remnant edge within adjacent mānuka. Each transect contained 14 seed traps of 50 cm diameter, for a total trap area per

transect of 11.00 m^2. I sought to mimic the receiving environment (including risk of seed predation), so traps were not covered with mesh or other material that would exclude predators. Seed trap contents were collected approximately every two months, dried, and plant species identified and counted for each seed found in a trap. The final seed collection was in December 2014.

I compared which species had produced seed within the remnant to the seeds found within the mānuka. I provide a quantitative description of the presence or absence and amount of seeds found in the results.

Seed sowing experiment

Seed limitation can be diagnosed using sowing experiments (Turnbull, Crawley & Rees 2000). Turnbull , Crawley & Rees (2000) note that in such an experiment, if no establishment occurs, it may be because no suitable conditions exist for seeds to germinate, or that seed predation has occurred. Recruitment indicates that abiotic conditions are suitable and that the absence of species can be attributed to lack of seed dispersal.

Seed sowing experiment: overview

The sowing experiment was undertaken at the two 'low dispersal' sites from the vegetation survey – Tiwai and Clearwater. The experiment was a nested, split-plot design. I tested the effects of canopy using pre-existing vegetation mapping in the wetland, which had classed the mānuka into either 'semi-open' or 'dense' based on canopy openness. I created a third type, 'thinned', to separate existing correlated abiotic conditions with canopy openness by thinning dense canopies. At each site, I had 12 plots, consisting of four plots of each canopy type (Figure 2.3).

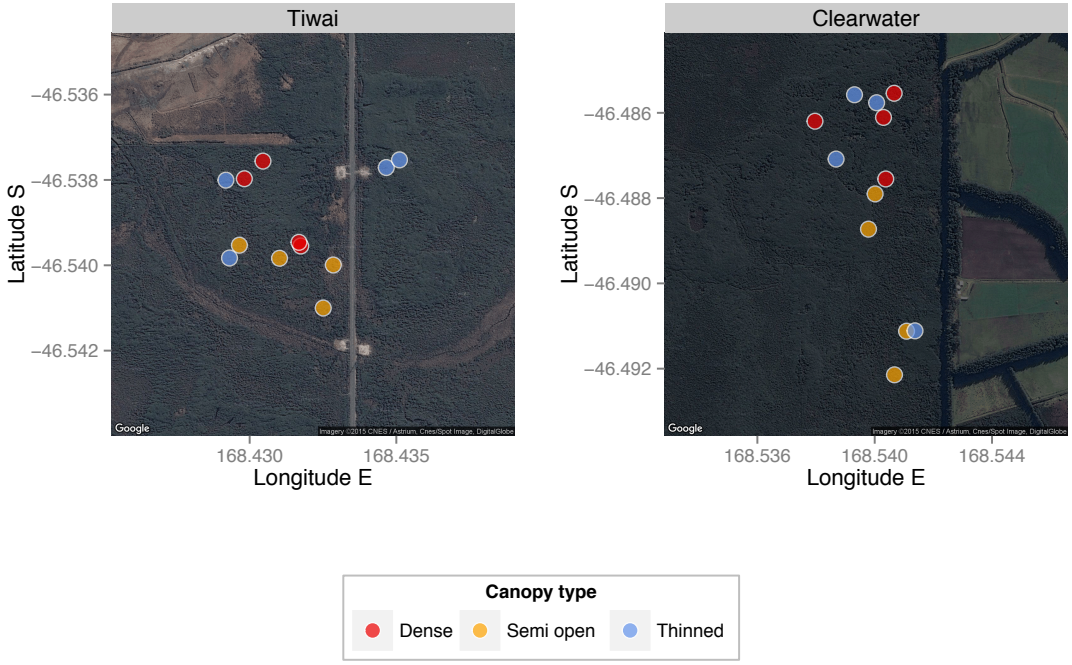


Figure 2.3: Sowing experiment sites. The grey line at Tiwai is Tiwai Rd. Underlying map sourced from GoogleEarth, October 2015.

Each plot was split into understorey treatments ("sub-plots"). Each sub-plot contained four sowing treatments ("replicates"): sown, caged; sown, uncaged; unsown, caged; unsown, uncaged (Figure 2.4).

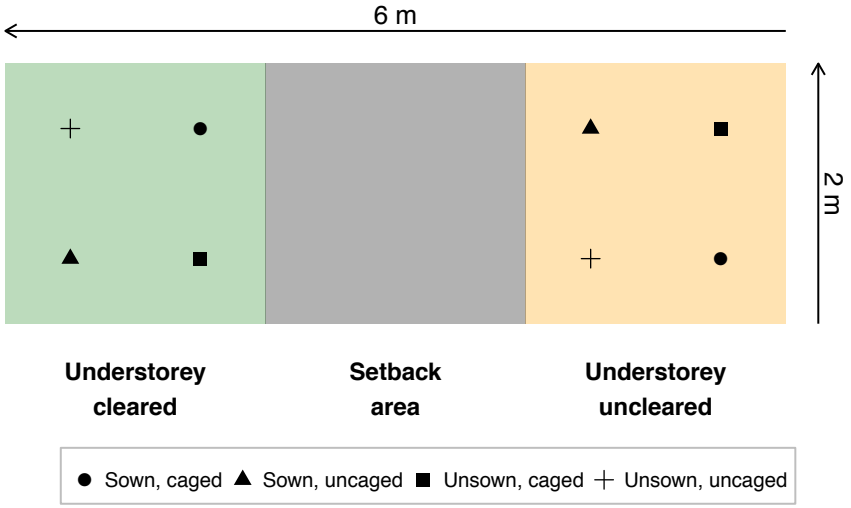


Figure 2.4: Example of seed sowing experiment plot layout. Twenty-four plots were set up in total, twelve plots at each site. The twelve were split into four of each canopy type (dense, semi-open, thinned).

Seed sowing experiment: fieldwork

The sowing experiment was set up over four consecutive days of clear weather in June-July 2011. Plots were chosen randomly using ArcGIS and existing canopy mapping (Anon. 2010). I included a 20 m minimum separation distance between each plot and a 50 m set back from site edges. Points were randomly selected using ArcGIS and loaded on to a handheld GPS, and subsequently located in the field. Where points were found not to be in mānuka (the mapping was based on aerial photography), I chose the nearest area of mānuka canopy to establish each plot. I then undertook a coin toss to select the orientation of each plot (north-south or east-west). I marked out the entire plot area (6 x 2 m) and sub-plot areas (each sub-plot measured 2 x 2 m, separated by a 2 x 2 m setback area in the middle). I conducted a second coin toss to decide whether the first (north or east) sub-plot was cleared or uncleared understorey (Figure 2.4). In the centre of each sub-plot I measured the height to canopy from the centre of the sub-plot using a tape measure, and then where the canopy treatment was "thinned", selected and cut down the central mānuka stem. After this, I measured canopy openness using the same protocol as for the vegetation survey. The sub-plot in which the understorey was cleared involved the removal (manually and using clippers where required) of vegetation under 30 cm, such as *Empodisma minus*, *Carex* species and *Pteridium esculentum*. Disturbance to the soil and litter layers was minimised.

Within each sub-plot I had four replicates to setup (sown, caged; sown, uncaged; unsown, caged; unsown, uncaged). I used random numbers to allocate the arrangement of treatments to replicates in advance. Each sown replicate (caged and uncaged) was sown with 140 seeds, consisting of 30 *Griselinia littoralis* seeds, 20 *Aristotelia serrata* seeds, 20 *Carpodetus serratus* seeds, 20 *Melicytus lanceolatus* seeds, 20 *Pseudopanax crassifolius* seeds, 20 *Raukaua simplex* seeds and 10 *Pittosporum tenuifolium* seeds. Seeds were locally sourced from forest remnants within 30 km of the wetland and refrigerated until sowing. To prevent seeds rolling away seeds were sown into 10 cm diameter tubes of 4 cm wide

strips of lexan polycarbonate (1 mm thick) with the ends stapled together. Tubes were inserted into the soil approximately 50 cm apart with around 2 cm of the tube remaining above ground. For each caged replicate I constructed 10 cm high mammal-proof cages using 5.8 mm aperture stainless steel weldmesh. Cages and tubes were secured to the ground with wire pegs. Unsown tubes provided 0.754 m^2 (96 replicates multiplied by 0.008 m^2 for each tube) total of area in which seeds might naturally fall.

I counted the number of seedlings germinated and surviving approximately every two months beginning in December 2011, until the experiment ended in February 2014. I measured the heights of survivors and seedling survival counts in the final experiment count in February 2014.

Environmental data were collected at the plot and sub-plot level at the time of establishment, except for canopy age, stem diameter and soil samples, which were collected in February 2013. Canopy openness and height to canopy have already been described above in the setup procedures. I measured depth to groundwater, soil moisture and soil conductivity using the same methods as for the vegetation survey. Age of canopy and stem diameter were measured and soil samples collected over four days in February 2013. Age and stem diameter were sampled by choosing a representative (i.e. average sized) mānuka stem approximately two metres at right angles from the central 2 x 2 m plot area. Stems were felled and growth rings counted at 30 cm above ground height. Soil samples were collected over a period of four days using a standard 10 cm soil core, bagged, sealed and stored in an insulated container until all had been collected, after which they were sent immediately to Landcare Research New Zealand Ltd environmental chemistry lab in Palmerston North where they were analysed for the following parameters: dry bulk density, water content (% of dry weight), pH (1:5 water), electrical conductivity (dS/m), organic carbon (%), total nitrogen (%), carbon-nitrogen ratio, total P (mg/kg).

Seed sowing experiment: analysis

No forest species established in my control plots, which led to complete data separation. Therefore no statistical analyses were undertaken of the control (unsown) plots. The canopy type, understorey clearance and caging treatments were fully orthogonal, which allowed me to test for interactions between treatments. I tested the effect of canopy type and understorey clearance on seedling survival, and an index of biomass (summed seedling height of each replicate, hereafter biomass). I tested the effect of caging on seedling survival and biomass, as for canopy and understorey, but as New Zealand herbivorous mammals can affect species differentially due to dietary preferences (Nugent *et al.* 2000), I also tested the species richness and diversity of each replicate. All four responses were analysed using generalised linear mixed effects models in R using packages LME4 (Bates *et al.* 2014) and GLMMADMB (Skaug *et al.* 2014). The data were visually inspected and transformed where necessary. All models included a random intercept that reflected the experimental design (caging treatment nested within understorey treatment nested within canopy type nested within site). For each model I present the full model (additive effects of canopy type, understorey clearance and caging, and all interactions thereof), and the best reduced model. I tested for the best model by comparing all possible subsets of the full model using the Information-Theoretic Model Comparison approach (Burnham & Anderson 2002). Models were compared using Akaike's Information Criterion for small sample sizes (AICc) which maximises fit to the data while penalising overfitting; delta AIC indicates the difference between the 'top' model and subsequent models using package MUMIN in R (Bartoń 2014).

The survival model tested the number of seedlings surviving as a proportion of the total sown, at each replicate (n = 140) and by species (all species n = 20, except: *G. littoralis* was sown at n = 30 at all sown replicates and *P. tenuifolium* was sown at n = 10 at all sown replicates). The biomass model tested the sum height of seedlings at each replicate with a Gaussian distribution following a square root transformation. I tested species richness (the number of species) and diversity (Shannon Index) by calculating the richness and diversity for each replicate with a Gaussian distribution.

I tested whether the seed sowing experiment adequately covered the environmental range of the 160-plot vegetation survey by ordinating the environmental conditions at the seed sowing sites against those found in the vegetation survey, replicating the same transformations and methods. To do this I used supplementary data collected over three fine days in 2012 (10 – 12 December 2012). I sampled all 24 seed sowing plots (n = 12 at each site), and 46 vegetation survey plots (n = 11 for Craws Creek and Lawsons; n = 12 for Tiwai and Clearwater, plots within each site chosen randomly). Equipment failure (soil moisture meter breakage) meant I was unable to obtain 12 samples for each vegetation survey site. I collected data on soil moisture, soil conductivity and depth to groundwater using the same methods applied in the vegetation survey and seed sowing experiment.

To disentangle the relative contributions of the abiotic and biotic environment to seedling survival and biomass, I undertook variance partitioning, which separates the unique and common contributions of groups of variables to the community response (Peres-Neto *et al.* 2006). This is a constrained multivariate analysis, which allows for species to vary in their response to treatment effects and biotic and abiotic conditions. I categorised the explanatory variables into three groups: facilitative variables relating to the mānuka canopy under which the seedlings grew; abiotic (soil) conditions; and manipulated treatments. Facilitative variables consisted of canopy height, canopy age, and log canopy openness; abiotic (soil) conditions were depth to groundwater, pH, total phosphorus and total nitrogen; fixed effects were canopy, caging, understorey, and second-order interactions thereof. In the results I present Euler diagrams, where the size of the circle and the size of circle overlaps are proportional to the variance explained (specifically, r-squared). I present the adjusted r-squared for each fraction (e.g. facilitative effects are presented controlling for the effects of abiotic variables and fixed effects). Fractions of < 0 are not labelled; fractions are given to two decimal places.

To complement the multivariate analysis, I also tested the importance of abiotic filters on the univariate responses of seedling survival and growth. I tested the relative importance of natural environmental gradients against the biotic effects using the Information-Theoretic Model Comparison approach (Burnham & Anderson 2002). I compared a subset of likely models, with variables tested individually and in groups (see details in Appendices 2.7 and 2.8). Models were compared using Akaike's Information Criterion for small sample sizes (AICc) which maximises fit to the data while penalising overfitting; delta AIC indicates the difference between the 'top' model and subsequent models. I present the 'best' model according to AICc with predicted treatment effects and 95% confidence intervals. I predict only within the range of raw data for each canopy type. Confidence intervals are calculated on the basis of fixed effect uncertainty only. Model selection tables for all models for which delta AICc was < 4 are presented in the appendices.

2.3 Results

Vegetation survey

The primary purpose of the vegetation survey was to quantify the amount of forest regeneration and correlated abiotic and biotic factors. A species list of all plant species found within the vegetation survey is provided in Appendix 2.1. The vegetation survey also provided an overview of the differences of vegetation composition between the sites.

I tested which species differed across sites using a multivariate generalised linear model, which provides adjusted p-values for multiple testing (package MVABUND (Wang *et al.* 2014)). I used site as the predictor and percent cover as the response. The species which differed significantly across sites (Figure 2.5) can be classed into three general groups: plants characteristic of wetlands, invasive plants, and native forest plants. Plants more typical of wetter environments (particularly *Gleichenia dicarpa* and *Empodisma minus*) had higher cover on average at Tiwai and Clearwater, and sphagnum species were only found at Clearwater and Craws Creek. Two species were found within the wetland that

pose a risk to native forest regeneration. Gorse (*Ulex europaeus*) and blackberry (*Rubus fruticosus*) were found at Tiwai - three plots contained *U. europaeus* only, three plots contained *R. fruticosus* only and three contained both. *Ulex europaeus* was found in one plot at the Clearwater site. Three forest species also differed significantly across sites. Full results are set out in Appendix 2.2.

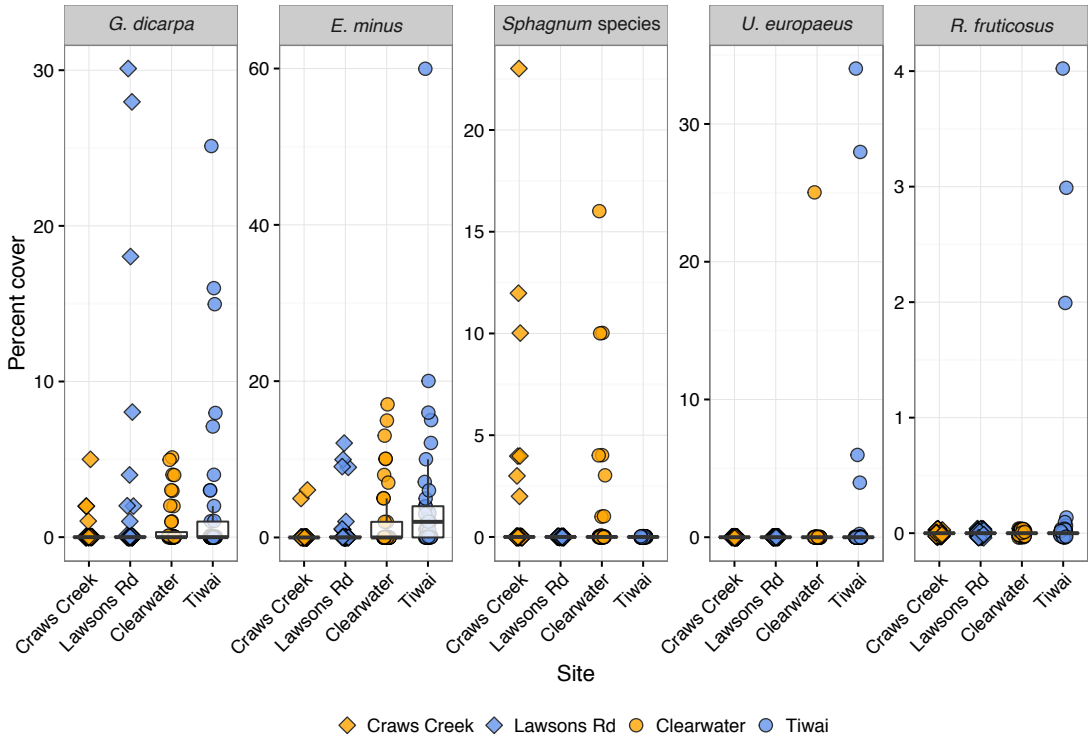


Figure 2.5: Percentage cover per plot of wetland species (G*. dicarpa*, *E. minus* and *Sphagnum* species) and invasive species (*U. europaeus*, *R. fruticosus*) which differed significantly in their cover across sites. Results of multivariate generalised linear models are presented in Appendix 2.2

Is forest regeneration within the wetland dispersal-limited? If so, at what scale?

At the site level, forest regeneration differed significantly (Figure 2.6). Craws Creek had the highest amount of regeneration in terms of number of plots containing regeneration, mean number of forest seedlings per plot, mean cover of forest species per plot, and mean total height of forest species per plot. The Lawsons site had more plots containing regeneration and more mean seedlings per plot than Clearwater, but less cover on average and total plot height was less. I consider the lower cover and height of regeneration at Lawsons is likely due to the intermittent presence of stock in the mānuka. Tiwai only contained one *Coprosma foetidissma* overhanging a plot. All means and standard errors are provided in Appendix 2.3.

I analysed forest regeneration both by the proportion of plots containing native forest species in (presence/absence) and by cover (%) of forest regeneration by site, using generalised linear models. The site adjacent to forest, Craws Creek, had significantly more plots containing regeneration than the other three sites (Lawsons Rd: $z = -3.700$, $p = 0.0002$; Clearwater: $z = -5.117$, $p < 0.0001$; Tiwai: $z = -5.242$, $p < 0.0001$). This was consistent with site-level distance to seed source (Craws Creek: adjacent; Lawsons: 350 m, Clearwater: 950 m, Tiwai: 2.4 km). Craws Creek had a significantly higher cover of regeneration per plot (Lawsons Rd: $z = -13.53$, $p < 0.0001$; Clearwater: $z= -13.47$, $p < 0.0001$; Tiwai: $z = -14.34$, $p < 0.0001$).

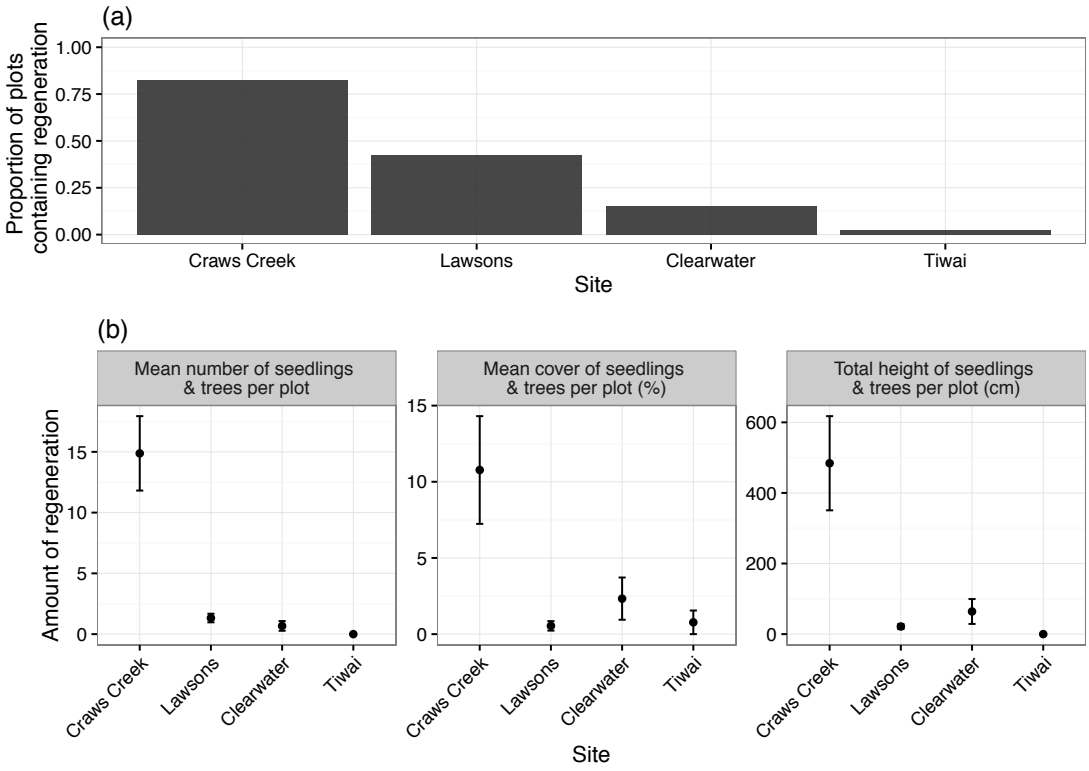


Figure 2.6: (a) The proportion of plots (of 40 at each site) containing forest regeneration. (b) From left to right: mean number of forest trees and seedlings per plot; mean cover of forest seeds and trees per plot (as a percentage); the summed height of all forest trees and seedlings on average at each plot. Seedlings below 1 m were binned into 10 cm bins. The amount of regeneration is consistently higher at Craws Creek, across all measures. Lawsons had more plots containing regeneration and more mean seedlings per plot, but less cover on average and total plot height was less there compared to Clearwater. All points in (b) are +/- standard error of the mean (raw data).

Within Craws Creek I tested whether distance to forest remnant or other environmental variables were most correlated with the number of forest species seedlings and their percentage cover. I tested these relationships using boosted regression trees, which use formulae developed by Friedman (2001) to estimate the relative importance of each of the predictor variables. Variable importance is based on how many times a variable is selected in each tree, and the improvement it makes to the tree's explanatory power, averaged over all trees. Relative influence is scaled to sum to 100, with high values awarded to variables with stronger influence. Distance to forest remnant was the most important variable correlated with the number of forest seedlings in each plot (relative importance: 82) and forest species' plot biomass (relative importance: 63). In both analyses canopy openness and a measure of soil moisture were the next most influential (Figure 2.7(a)).

The marginal effect of distance on forest species was non-linear Figure 2.7(b). The marginal effect of a variable in boosted regression is calculated by holding all other variables to their mean. Boosted regression trees differ from generalised linear models in that they can model complex, non-linear relationships (Elith, Leathwick & Hastie 2008). At approximately 230 m from the centre of the forest remnant, predicted forest species counts dropped from 20 to just over 5. At the same distance, total forest species heights within plots were predicted to decrease from 7 m to 2 m. This may indicate a threshold distance beyond which birds do not penetrate into the mānuka. The boosted regression tree could have up to third order interactions, but none were found, so only main effects are presented.

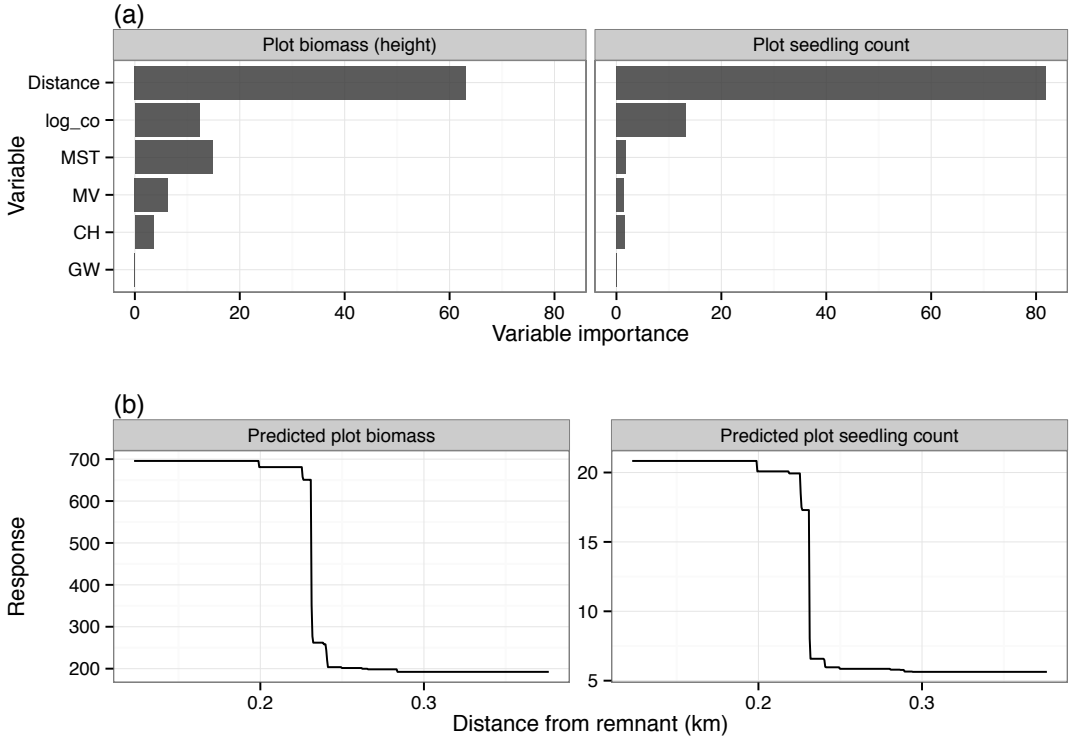


Figure 2.7: Effect of distance from podocarp-broadleaf forest and other factors on the quantity of native forest regeneration per plot in 40 plots at Craws Creek. (a) Distance from remnant is the most important variable in determining how much biomass (total height forest species' seedlings in plot in cm) and the number of seedlings a plot is likely to have. Variable importance is based on the percentage of regression trees the variable appeared in and how early in the tree it was chosen. Other variables (in order) are log canopy openness, % soil moisture, conductivity (MV), canopy height, depth to groundwater. (b) A sharp decrease in both biomass (total height forest species' seedlings in plot in cm) and number of seedlings is predicted at approx. 230 m from remnant edge.

Figure 2.8 shows the predicted, standardised spatial distribution of regeneration (plot biomass [total height forest species' seedlings in plot in cm] and plot seedling count) at the Craws Creek site, predicted on the basis of marginal effect of distance.

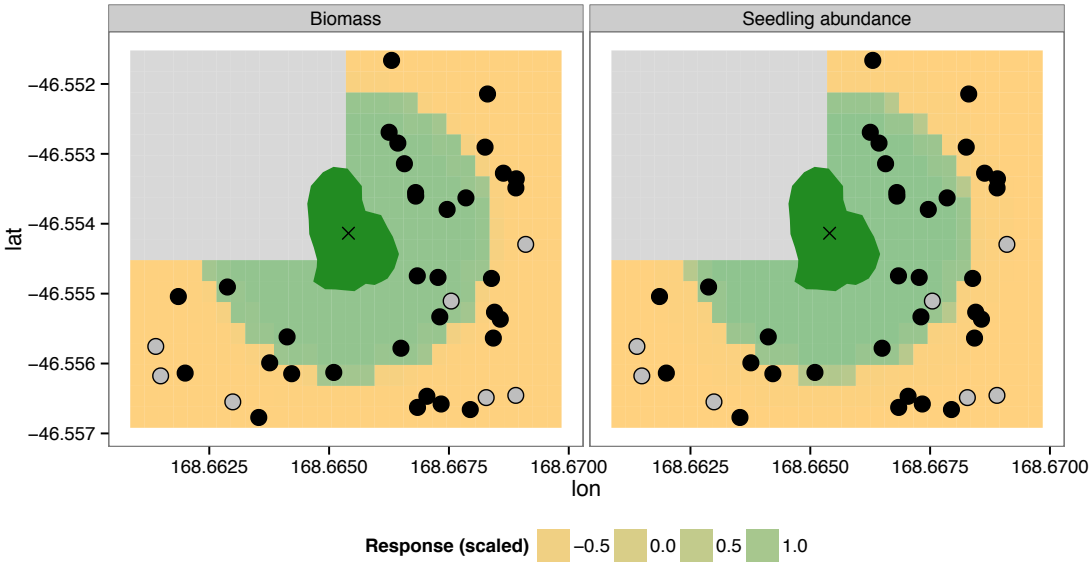


Figure 2.8: Standardised response of biomass (total height forest species' seedlings in plot in cm) and seedling abundance (number of seedlings) predicted to the site scale for visualisation. I used a standardised response because the two responses (biomass and seedling abundance) were on different scales. Standardising subtracts the variable's (e.g. biomass) mean from each data point and then divides each resulting data point by the variable's standard deviation, such that the mean is zero and one standard deviation is 1. The effect is that larger, more positive values indicate a higher predicted response for both response variables. The nor-west quadrat is excluded as it goes beyond the extent of raw data (plots were randomly allocated only within areas mapped as mānuka (Anon. 2010)). Grey points are plots which had no regeneration.

I predicted how much regeneration would be found at the other three sites, with a varying distance to a seed source (the same range as found at Craws Creek). Sites were all predicted to contain a similar amount of regeneration in total (Table 2.2).

Table 2.2: Mean numbers of seedlings seen in each plot in the vegetation survey (and standard error), compared to the predicted mean number of seedlings when sites are modelled to be as close to a forest remnant as Craws Creek. Craws Creek is included for comparison. The predicted differs to the original because I modelled all plots at Craws Creek along with the other sites.

Site	Mean number of seedlings per plot	se N	Predicted mean number of seedlings per plot
Craws Creek	14.88	3.06	15.46
Lawsons	1.33	0.36	16.70
Clearwater	0.68	0.40	17.32
Tiwai	0.00	0.00	15.21

Lawsons (next closest to seed source, but also subject to intermittent cattle grazing) was predicted to have environmental conditions allowing a higher amount of forest regeneration than Craws Creek. Tiwai and Clearwater were predicted to have less at all distances from forest remnant than Lawsons and Craws Creek (Figure 2.9).

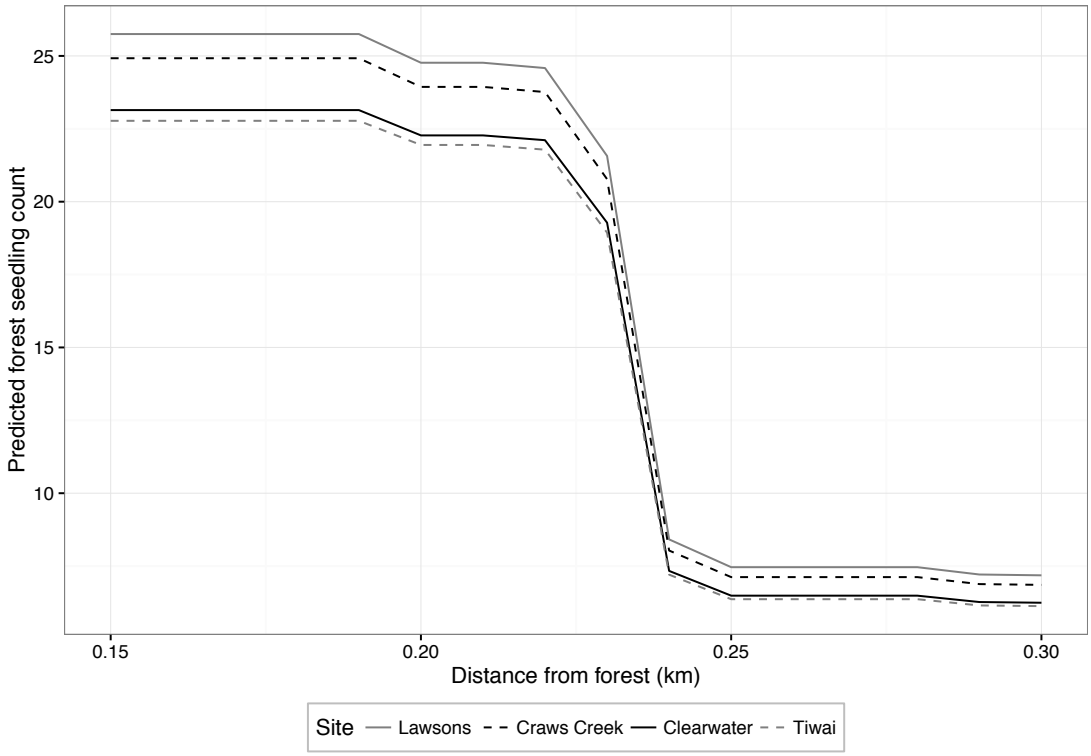


Figure 2.9: Predicted number of forest seedlings (y-axis) at Lawsons, Clearwater and Tiwai assuming they were as close to a remnant as Craws Creek, but with the existing environmental variables found at each vegetation survey plot. In the vegetation survey the highest mean seedlings per plot after Craws Creek was at the Lawsons site, with 1.33 seedlings (Table 2.2).

Although I could predict how much regeneration the Lawsons, Clearwater and Tiwai sites would have if they were as close to a remnant as Craws Creek, some plots within Clearwater and Tiwai were outside of the environmental conditions that were experienced at Craws Creek and Lawsons. I ordinated the environmental variables of the vegetation survey plots using non-metric multidimensional scaling and determined the environmental niche by calculating the hull around all data points in the high and low dispersal groups. I found some Tiwai and Clearwater plots were wetter, shorter and more open than any found at Craws Creek and Lawsons (Figure 2.10).

A more definitive finding in respect of seed limitation can be obtained from sowing seeds into niches considered to be seed limited, which I address in the seed sowing experiment results (below, following the seed trapping experiment).

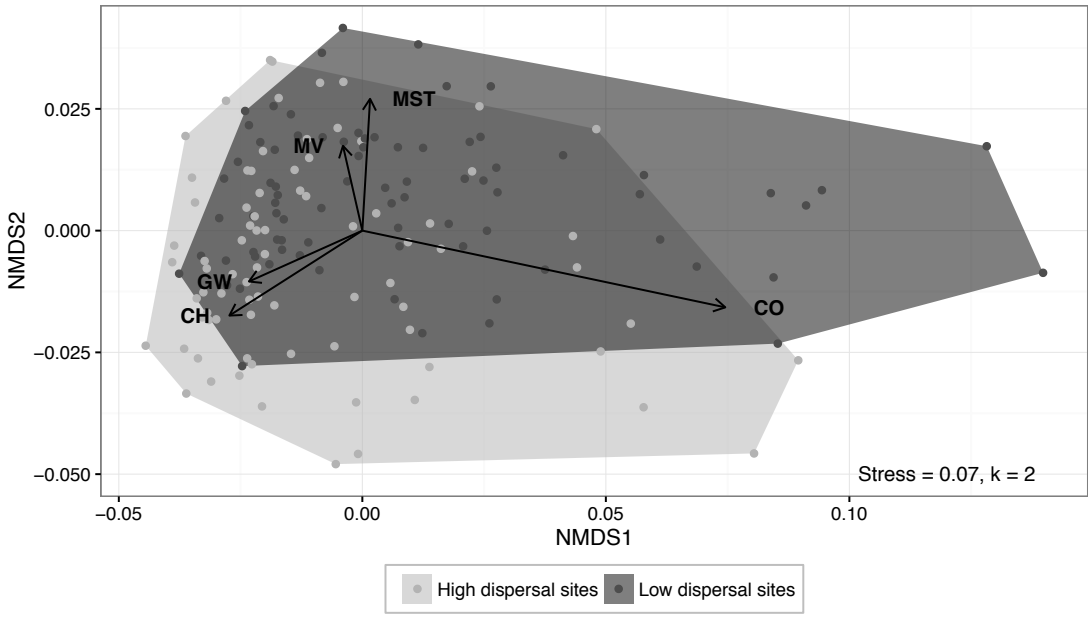


Figure 2.10: Environmental niche at high dispersal sites (Craws Creek; Lawsons Rd) and low dispersal sites (Clearwater; Tiwai). I ordinated the environmental variables of the vegetation survey plots using non-metric multidimensional scaling and determined the environmental niche by calculating the hull around all data points in the high and low dispersal groups. There were some plots in the low dispersal group which were outside the environmental range of the high dispersal group. These plots were wetter (associated with higher values of MST [soil moisture] and MV [soil conductivity]) and more open (associated with higher levels of CO [canopy openness]). Other abbreviations: CH = canopy height, GW = depth to groundwater.

Seed trapping experiment

I determined whether species within the forest fragment were being dispersed into areas of suitable habitat (the mānuka) by setting up seed traps within the forest remnant at Craws Creek and at increasing distances from it within surrounding mānuka.

Eight species (all bird dispersed) within the forest remnant were not found in any seed traps within the mānuka (Figure 2.11): *Myrsine divaricata, Prumnopitys ferruginea, Myrsine australis, Podocarpus cunninghamii, Prumnopitys taxifolia,*

Griselinia littoralis, Phyllocladus alpinus, Dacrydium cupressinum (Figure 2.11(a)). These eight species were all found to be producing fruit within the forest remnant. Of those species I found being dispersed within or into the mānuka, three (*Coprosma foetidissima, Pseudopanax crassifolius, Pittosporum tenuifolium*) were species of regeneration interest. For these species seed fall was so low it was essentially a binary response: very low within mānuka compared to within the remnant, but there was no strong pattern with increasing distance from remnant (Figure 2.11(b)). Other *Coprosma* species exhibited more of a continuous response to distance from the remnant (Figure 2.11(b)).

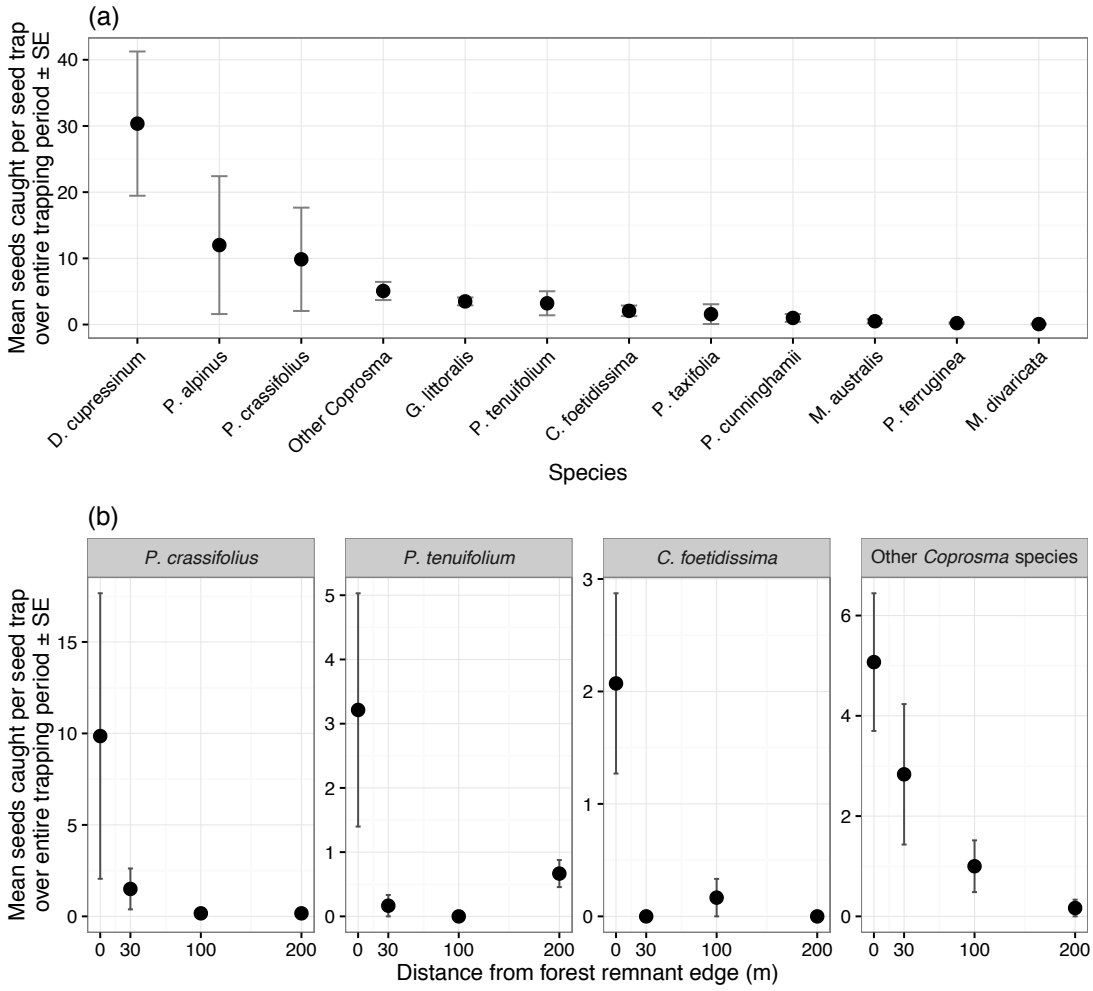


Figure 2.11: (a) Mean number of seeds per seed trap in the forest remnant only, identified over the entire trapping period, error bars indicate standard error around the mean. Full species names are: *Dacrydium cupressinum* (rimu), *Phyllocladus alpinus* (mountain toatoa), *Pseudopanax crassifolius* (horoeka), *Pittosporum tenuifolium* (kohuhu), *Coprosma foetidissima* (naupiro), *Prumnopitys taxifolia* (mataī), *Podocarpus cunninghamii* (tōtara kōtukutuku), *Myrsine australis* (māpou), *Prumnopitys ferruginea* (miro), *Myrsine divaricata* (weeping māpou). (b) Mean number of seeds per

seed trap identified over the entire trapping period. Error bars indicate standard error around the mean. Species abbreviations are as for (a).

These 2014 seed trap data are consistent with the relationship observed between seedling abundance of forest species and distance within the wetland (Figure 2.12), with one exception: *Griselinia littoralis*. *Griselinia littoralis* was the most abundant species in the vegetation survey (Figure 2.12), and was found within the forest remnant. There is no apparent reason why *G. littoralis* should have been found to be fruiting within the remnant in 2014 but failing to be found in the mānuka, despite it clearly having been dispersed into the mānuka previously. Other *Coprosma* species were not counted individually in the vegetation survey, but were present in 112 of all 160 vegetation survey plots and 30 of 40 plots surveyed within the Craws Creek site.

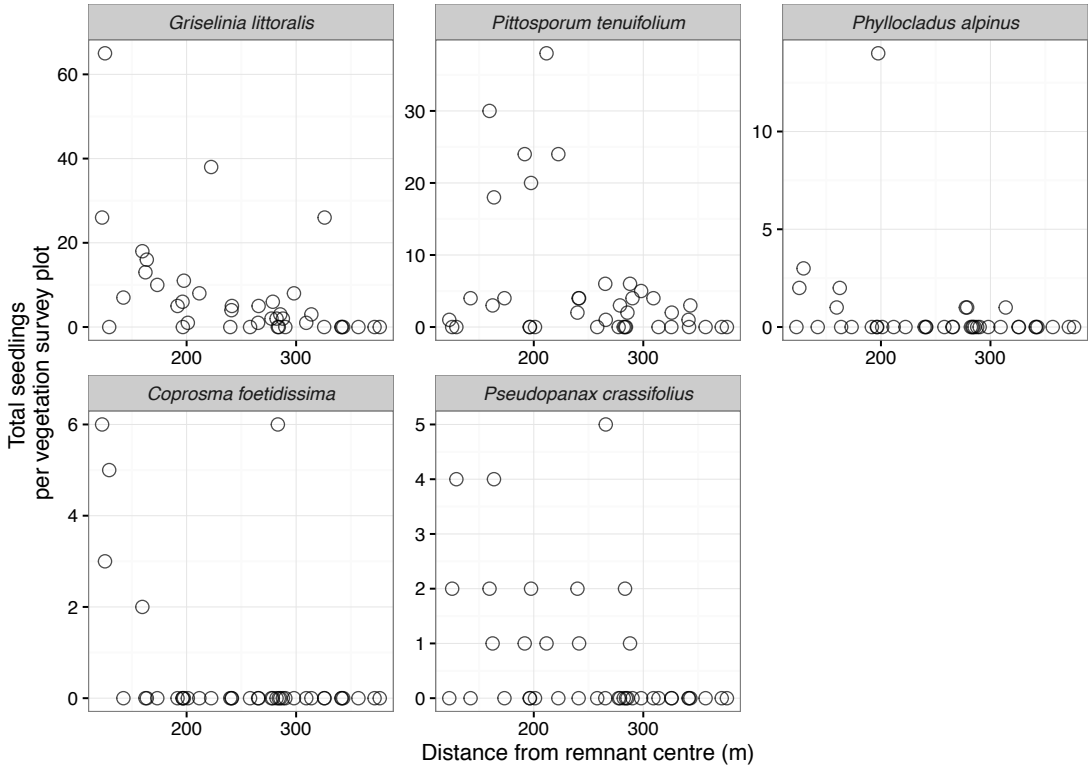


Figure 2.12: Vegetation survey raw data showing the total number of seedlings per plot on the y axis (note different y scales) and distance from remnant centre on the x axis. Each circle represents one vegetation survey plot. All later successional forest species found in the vegetation survey are shown.

Seed sowing experiment

Of the total 13,440 seeds sown across 96 replicates, 1,552 germinated and survived to be counted at the final survey (February 2014). Of the 1,552 surviving seedlings, 1060 were in caged treatments and 492 were uncaged. The maximum number of seedlings alive and counted in any one sampling period was 1,728 (January 2013). Of the 1,728 seedlings 1,121 were in caged treatments and 607 were uncaged. All six sown species germinated. The most abundant species was *Pseudopanax crassifolius*, of which 743 seedlings were surviving at the end of the experiment out of a total of 1920 sown seeds (96 plots x 20 seeds per plot). *Aristotelia serrata* and *Carpodetus serratus* were the poorest survivors, with both having only 8 seedlings at the end of experiment, out of a total of 1920 seeds sown per species.

Seedling establishment increased in the seed sowing experiment, satisfying the test in Turnbull, Crawley and Rees (2000). No seedlings established in the unsown replicates, indicating relatively strong seed limitation. Although total tube size into which seeds could naturally be dispersed was limited (0.754 m^2), this finding is supported by the vegetation survey results. Clearwater and Tiwai sites studied were generally suitable for forest species germination and establishment: at the replicate level, the worst survival rate for caged seedlings at the 2 years mark was six surviving seedlings. One replicate in the uncaged treatment had no seedlings survive (Table 2.3).

Table 2.3: Minimum number of surviving seedlings for each replicate in the seed sowing experiment, measured February 2014.

Canopy treatment	Understorey treatment	Caged	Uncaged
dense	cleared	10	1
dense	uncleared	6	0
semi-open	cleared	15	3
semi-open	uncleared	13	5
thinned	cleared	22	1
thinned	uncleared	18	2

The seed sowing experiment tested sown seeds in three experimental treatments (caging, canopy type and understorey clearance) to see which maximised seedling survival and biomass (total height forest species' seedlings in plot in cm). For each analysis I present the full model (response as predicted by caging, canopy type, understorey, and all associated second and third order interactions), and the 'best' reduced model, comparing all permutations of the full model using AICc. I discuss treatments in descending order of effect size: caging, canopy type, and understorey.

I tested the effects of caging to protect from seed predation and seedling herbivory on four response variables, all of which were measured at 2.6 years post-sowing: seedling survival; seedling biomass (total seedlings height of seedlings in cm); species richness; and species diversity. I used cages that excluded seed predators and herbivores, and so treatments are referred to as "caged" (protected from herbivores and seed predators) or "uncaged" (not protected).

Caging significantly increased seedling survival across all species under both full and 'best' models ($z = -4.24$, $p < 0.000$ and $z = -8.282$, $p < 0.000$ respectively, see Appendix 2.4 and Table 2.4). Caging seedlings doubled their survival rate (across all canopy types and understorey treatments), increasing from an average of 7.3% seedling survival in uncaged replicates to 15.8% average

survival in caged replicates. I tested species-specific interactions by modelling survival as a function of species, species-specific canopy effects and species-specific caging effects. I present predicted means and confidence intervals in Figure 2.13(b). Under the species-specific model, caging was beneficial for all species, and significantly beneficial for *P. crassifolius* and *P. tenuifolium* (model summary provided in Appendix 2.4).

Table 2.4: Mean effect size of canopy type and caging (raw data): percentage of seedlings per plot surviving, of total sown. Standard error is in brackets.

Canopy type	Caged	Uncaged
Dense	11.9 (1.0)	4.8 (1.2)
Semi-open	17.1 (1.3)	9.8 (1.3)
Thinned	18.3 (0.8)	7.4 (1.3)

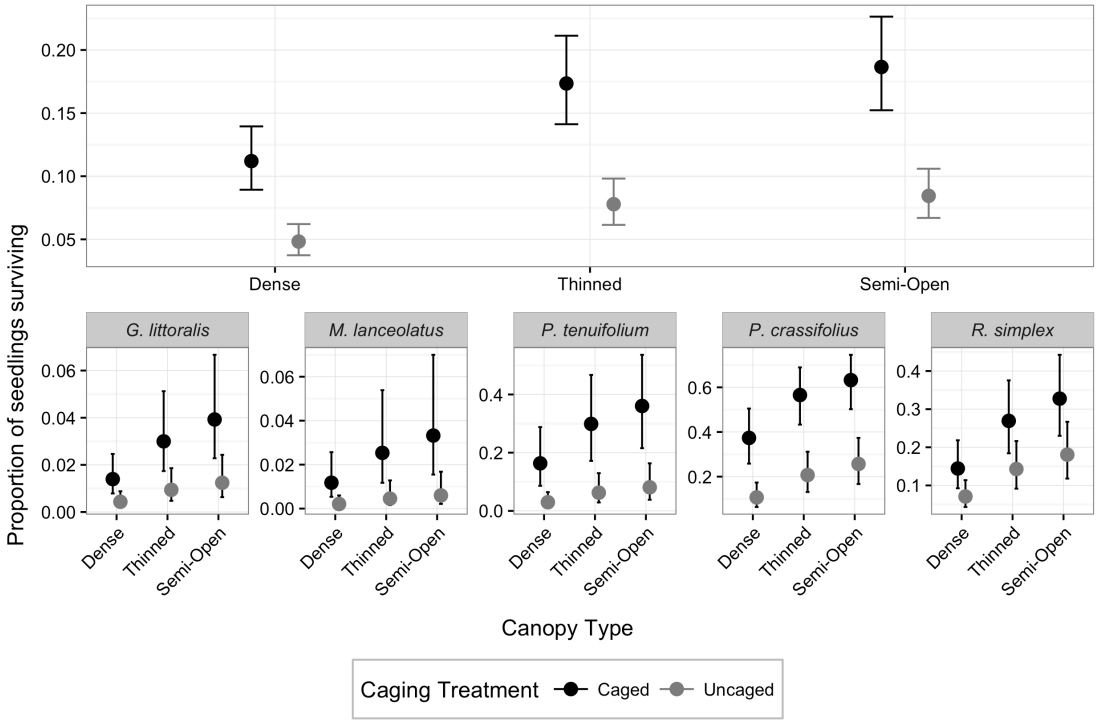


Figure 2.13: Effects of canopy type and caging treatments on seedlings survival - results of generalised linear mixed effects 'best' model according to AIC for all species (top) and by species. The best model for all species included the additive effects of caging and canopy only, while the best model by species included additive effects of caging, canopy, understorey and species, and a caging by species interaction. The uncleared understorey treatment is shown for visual simplicity only.

Error bars are the 95% CIs around the predicted mean. Two species (*A. serrata* and *C. serratus*) excluded from model because there were insufficient survivors to model effects.

Caging significantly increased the total biomass (total height forest species' seedlings in replicate in cm) of plots under both full and best models ($z = -4.42$, $p < 0.000$ and $z = -5.64$, $p < 0.000$ respectively, see Appendix 2.5 and Figure 2.14). Which canopy type seedlings were in modified the effect of caging – uncaged seedlings did somewhat worse in thinned canopies compared to dense (estimate = 0.8, $z = 0.87$, $p = 0.4$) and significantly worse than in semi-open canopy types (estimate = 1.9, $z = 2.14$, $p = 0.03$). When I attempted to analyse heights by species and compared models using AICc, I encountered model convergence issues, and I do not present species-specific results for biomass.

Because some species are more palatable to herbivores than others (Nugent, Fraser & Sweetapple 2001), I tested whether the species richness and diversity (Shannon index) differed due to caging. Uncaged replicates had on average 2.9 ± 0.21 (mean ± SE) species present per plot at the end of experiment measure compared to caged replicates that had on average 4.6 ± 0.17 species. Caging replicates led to significantly greater species richness based on the Shannon index ($z = 3.88$, $p = 0.001$ [full model reported only]) and evenness ($z = 3.50$, $p < 0.001$).

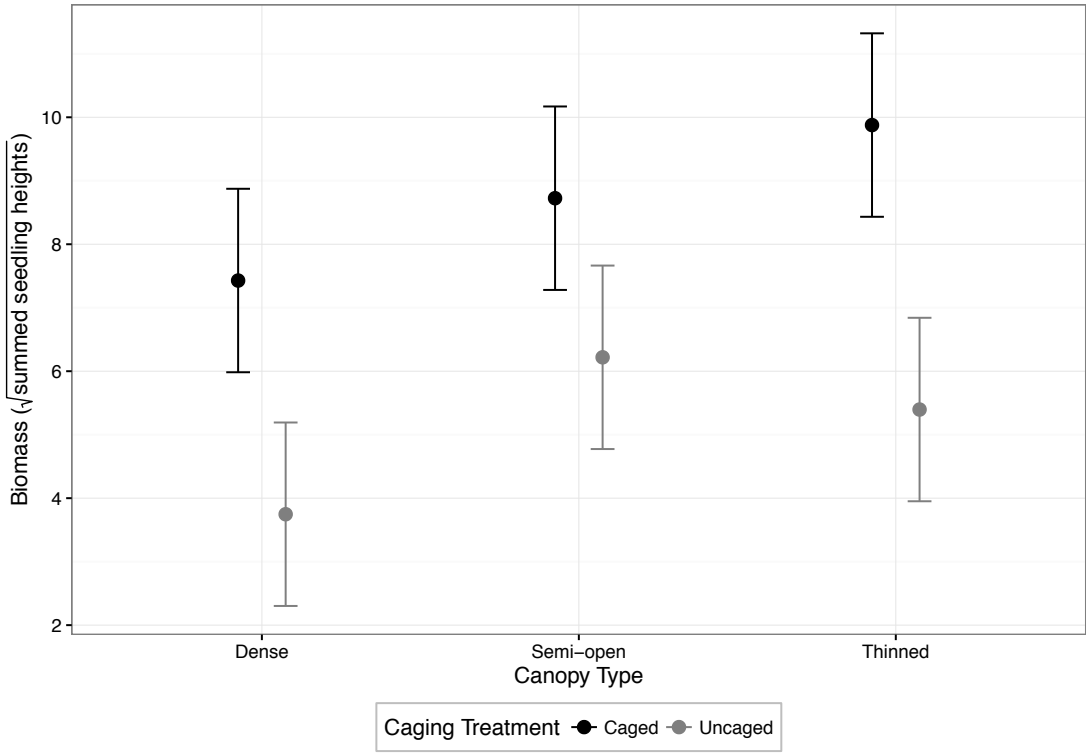


Figure 2.14: Effects of canopy type and caging treatments on seedling biomass (total seedling height in replicate in cm) - results of generalised linear mixed effects 'best' model according to AICc for all species. Error bars are the 95% CIs around the predicted mean.

The effect of canopy type was tested to see whether existing vegetation mapping might guide conservation efforts. The existing mapping included “dense” and “semi-open” types, based primarily on aerial mapping. I created a third type (“thinned”), by thinning dense canopies. I collected information on whether the canopy types differed in terms of their canopy openness, height and age in order to help explain any differences in treatment responses (Figure 2.15).

Thinned canopy types had more open canopies on average than dense (5.5% canopy openness vs 3.9% canopy openness), but both were substantially less open than semi-open canopy types (mean = 16.6% canopy openness). Dense and thinned canopy types were of a similar height (means of 4.3 and 4.5 m respectively), whereas semi-open canopies were shorter (mean of 3.3 m). All canopy types were of a similar age (means ranged between 29 and 34 years), based on tree-ring aging.

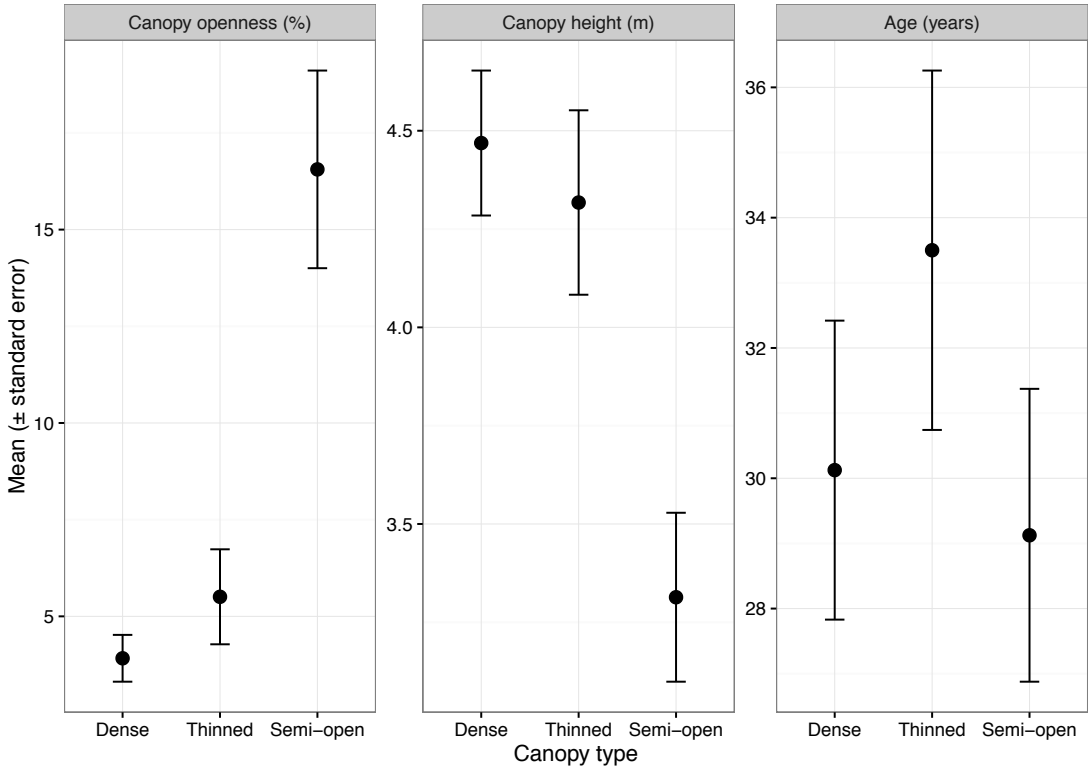


Figure 2.15: Key environmental variables of seed sowing experimental plots. Canopy openness is the percentage of the canopy open to the sky, measured with hemispherical photography. Canopy height was measured from the ground to the top of the canopy in the centre of each sub-plot. Age was estimated by cutting a representative mānuka individual and counting the tree rings. Dense and thinned are within one standard error on each variable; semi-open plots were more open and shorter on average. All plots were of a similar age. Note different y scales.

Seedling survival was significantly higher under thinned canopies across all species compared to dense canopies, under the 'best' model only (full model: $z = 1.893$, $p = 0.058$ and $z = 3.14$, $p < 0.001$ respectively, see Appendix 2.4). Semi-open canopies had increased seedling survival compared to dense, which was non-significant for the full model and significant for the reduced ($z = 1.446$, $p = 0.14$ and $z = 3.987$, $p < 0.0001$, respectively).

Seedling biomass (total seedling height in cm) was significantly greater under thinned canopies than dense canopies ($z = 2.12$, $p = 0.03$; and $z = 3.05$, $p < 0.005$ for full and reduced models respectively, see Appendix 2.5), while semi-open canopies did not differ significantly from dense canopies ($z = 0.84$, $p = 0.4$ and $z = 1.6$, $p = 0.1$ for full and reduced models respectively).

There was a significant species by canopy type interaction in the survival analysis (Figure 2.13, and Appendix 2.6). This was driven by significant differences in two species – *R. simplex* ($z = 2.95$, $p = 0.003$ for semi-open canopies, in which it survived significantly better), and for *P. tenuifolium* in thinned canopies, in which it survived significantly better than dense canopies ($z = 2.0$, $p = 0.046$).

Our understorey clearance treatment did not yield any significant differences in species survival or growth, or species richness or evenness. There was a variable amount of understorey to clear (personal observation), suggesting that suitable microsites exist in the wetland and clearance is not needed to create more.

As noted above, it was difficult to extrapolate from the vegetation survey to very 'boggy' plots at low dispersal sites (Figure 2.10). In order to compare the environmental variables from the vegetation survey and seed sowing, I remeasured the depth to groundwater, soil moisture and soil conductivity at 70 plots (all seed sowing plots and 46 vegetation survey plots) in December 2012. I conducted an ordination of the plots. The seed sowing experiment niche covered the wetter, more open plots (Figure 2.16) from low dispersal sites in the vegetation survey. This allows a synthesis of the findings of the vegetation survey and sowing experiment (see Discussion).

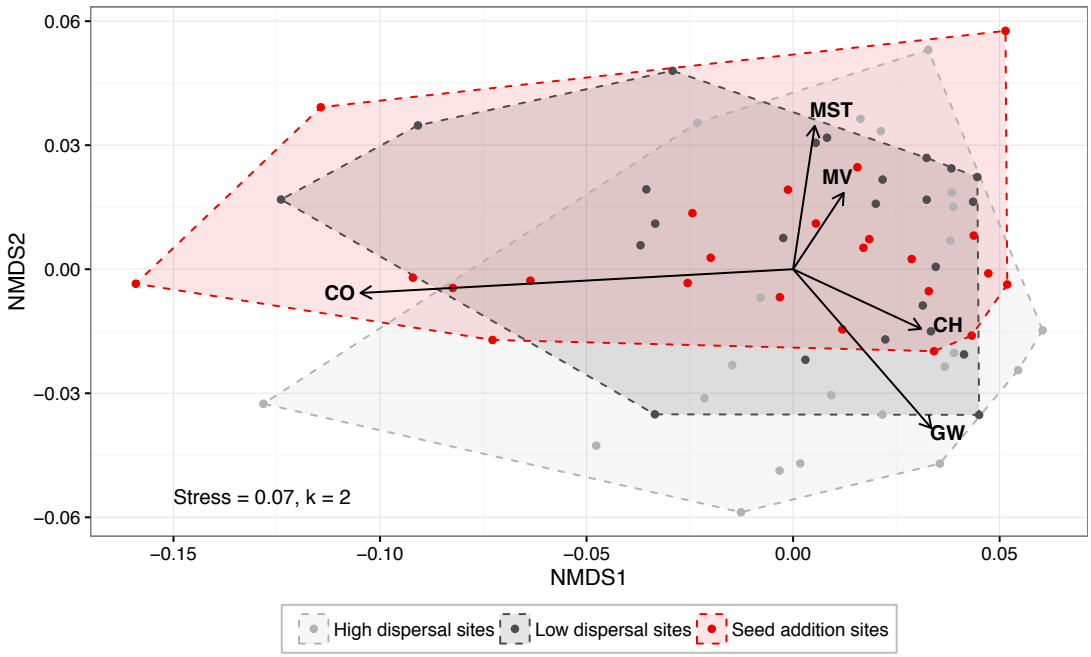


Figure 2.16: Ordination (NMDS) showing the environmental niches of the high dispersal sites (Craws Creek, Lawsons), low dispersal sites (Clearwater, Tiwai) and the sown seedling plots at the low dispersal sites (Clearwater, Tiwai). Environmental variable centroids are shown with arrows. MST = soil moisture, MV = soil conductivity, CO = canopy openness, CH = canopy height, GW = depth to groundwater.

To disentangle the relative contributions of the abiotic and biotic environment to seedling survival and biomass (total seedling height), I undertook variance partitioning, which separates the individual and joint contributions of sets of variables to the community response. This is a constrained multivariate analysis, which allows for species to vary in their response to treatment effects and biotic and abiotic conditions.

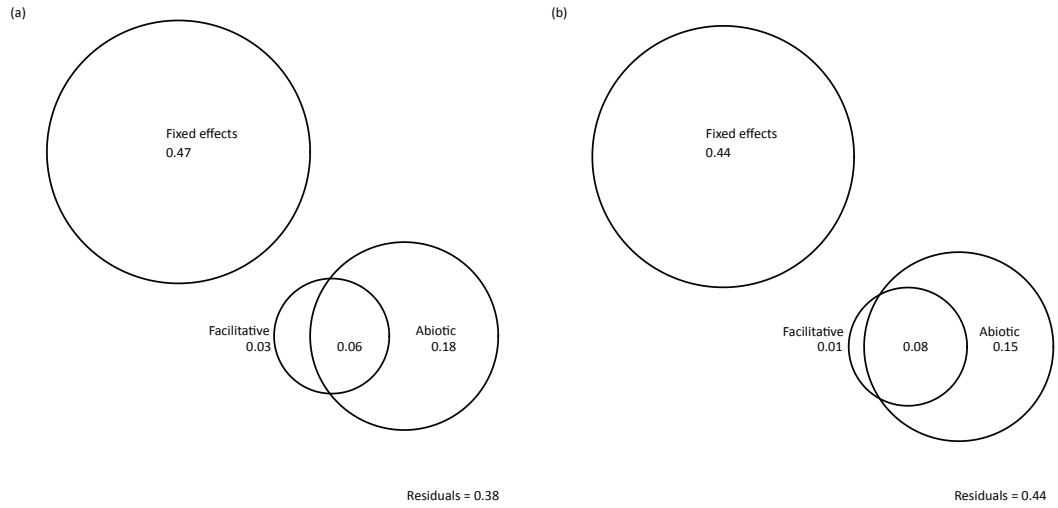


Figure 2.17: Results from the variance partitioning analysis, testing the contribution of groups of variables (fixed, abiotic, and facilitative) to explained variation in (a) seedling survival and (b) seedling biomass (total seedling height per replicate). The number in or adjacent to the circles are the adjusted r-squared of each fraction having partialled out other fractions. Area of circles (or fraction thereof) is proportional to the variation explained. For example, fixed effects explain 47% of the variation in seedling survival having accounted for the variation in environmental conditions and mānuka. Overlap between circles indicates shared contribution to explained variation. Experimental manipulation (the fixed effects) had the greatest effect on (a) seedling survival and (b) seedling biomass.

I categorised the explanatory variables into three groups: facilitative variables relating to the mānuka canopy under which the seedlings grew; abiotic (soil) conditions; and manipulated fixed treatments. The fixed treatment effects (canopy, caging, understorey and associated second order interactions) explained 47% of the variation in species survival, and 44% of variation in species biomass, after accounting for differences in the soil and mānuka (Figure 2.17). These were the highest proportions of variance explained for each response. There was a small shared contribution from the facilitative and abiotic conditions which is to be expected, given that the height and openness of the mānuka canopy are likely to co-vary with soil conditions.

To complement the multivariate analysis I quantified the effect of biotic and abiotic variables on the univariate responses of seedling survival and biomass (total seedling height per replicate in cm) using the Information-Theoretic Model Comparison approach (Burnham & Anderson 2002). I ran a subset of all possible combinations of predictors that I considered to be plausible (n = 32). The 'best'

model was selected using AICc; delta AICc indicates approximately how much worse a model is than the model before it. Appendices 2.7 and 2.8 provide full details of the analysis, including model selection table. For both seedling survival and biomass, the best models included canopy, caging and pH. The second best model for seedling survival was nearly equivalent to the pH model (delta AICc = 1.47), whereas the second best model for biomass included canopy openness, canopy height, and interactions between canopy and canopy openness and canopy openness and height (delta AICc = 2.46). Increasing pH (i.e., less acidic soils) had a significantly positive effect on seedling survival ($z = 43.36$, $p = 0.001$) and biomass ($z = 4.48$, $p < 0.000$, Figure 2.18). Caging remained significantly positive for seedling survival ($z = 5.7$, $p < 0.000$) and growth ($z = 6.29$, $p < 0.000$), semi-open canopy types had significantly more seedlings surviving ($z = 2.97$ $p = 0.003$) and held significantly more biomass ($z = 3.24$, $p = 0.001$), thinned canopy types had more survivors ($z = 1.7$, $p = 0.09$) and held more biomass ($z = 1.07$ $p = 0.2$) but neither difference was significant. The effect of pH varied significantly across canopy types for both seedling survival and seedling biomass: increasing pH was significantly less positive for semi-open canopy types than dense (seedling survival: $z = -2.72$, $p = 0.007$; seedling biomass: $z = -3.04$, $p = 0.002$) and less positive but not significantly so for thinned canopy types (survival: $z = -1.37$, $p = 0.16$, seedling biomass: $z = -0.6$, $p = 0.6$).

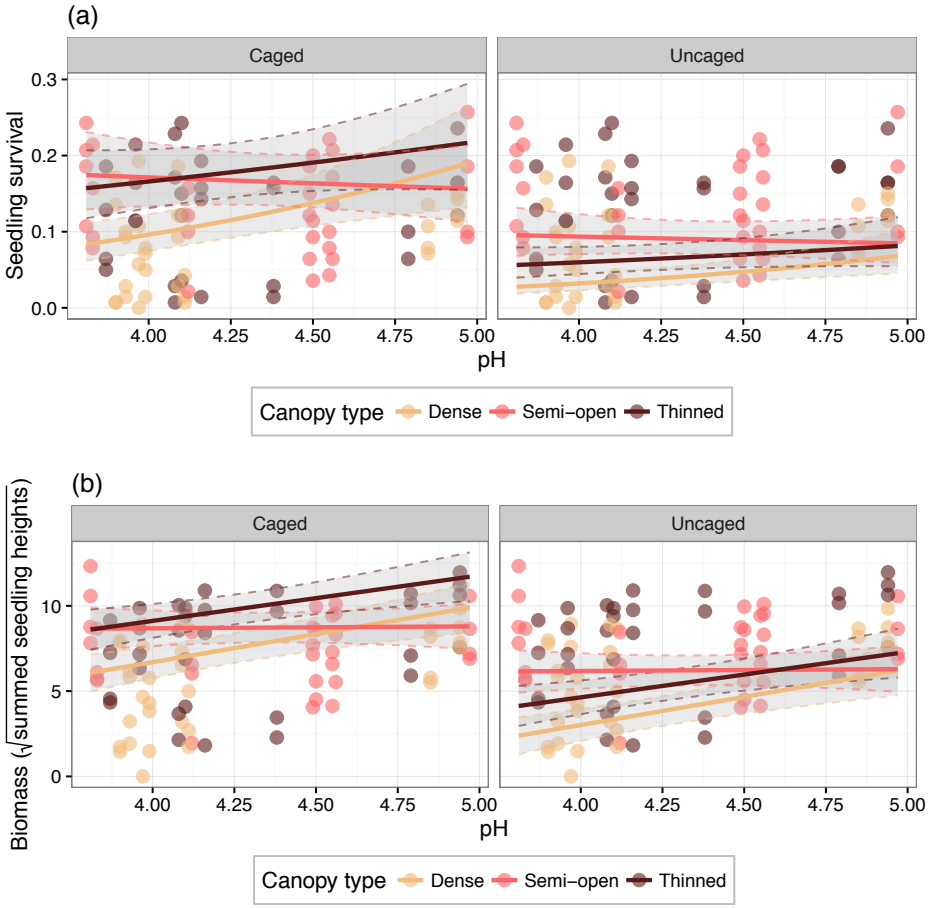


Figure 2.18: Results of 'best' models from model selection using generalised linear mixed effects models of fixed and environmental variables for the responses of (a) Seedling survival measured as proportion of seedlings surviving from the 140 sown at each replicate and (b) Plot biomass is measured as total replicate height (cm) of surviving seedlings, with a square-root transformation to normalise the distribution. Dashed lines and grey shading indicate 95% confidence intervals based on fixed effect uncertainty only. Each circle indicates one (raw) replicate from the experiment. Effects of pH are consistently positive for dense canopy types, but less so for thinned and semi-open canopy types.

2.4 Discussion

Overall, I found that seed limitation, dispersal limitation where seed sources exist, and biotic constraints (in particular, seed predation and seedling herbivory) are combining to slow, if not stall, regeneration after fire and clearance within Awarua wetland. Few forest seeds are being dispersed into suitable, available microsites and if dispersal did increase it would be strongly discounted by the effects of seed predation and seedling herbivory.

Seed and dispersal limitation

Dispersal was apparently functioning well at small scales, when I compared the presence or absence of regeneration at a small scale. Craws Creek, a site abutting a forest remnant, had a relatively high proportion of regeneration present in plots, and a height structure indicating recent dispersal and seedling establishment had occurred. At other sites, the presence of regeneration was much lower. However, even at Craws Creek, distance from seed source was the variable most correlated with the number of forest seedlings seen and the total biomass of each plot. I found evidence from the seed traps that some species present in the forest remnant and capable of growing in the wetland (*P. alpinus*, *G. littoralis*) are not being dispersed each year (or at least, in the period I surveyed). I found evidence of seed limitation rather than abiotic filters in the seed sowing experiment, at two sites of low natural dispersal, in which all caged plots had seeds germinate and seedlings establish, and in which no seeds arrived naturally and established as seedlings in the control plots. While we have seed trap data for only one site in the wetland, for one year, this 'snapshot' of dispersal certainly highlights that viable seeds of some species are not being dispersed into seed traps, or even as ephemeral seedlings (< 10 cm) in unsuitable abiotic environments. Though the results from Craws Creek are only from one site, this is the largest forest remnant within the wetland under public ownership. Craws Creek should therefore be a best-case indicator of the dispersal services smaller remnants will be receiving around the wetland or as pockets in agricultural areas.

Biotic constraints

Dispersal is a fundamental constraint on forest regeneration, because seeds must first arrive before they can be subject to any other constraining filters. Seed predation and seedling herbivory were the strongest biotic filters I measured in the seed sowing experiment on seed germination, seedling survival and seedling growth. Possums and rats are most likely responsible for the predation and herbivory, as they were the most common species found in the pest survey

(Chapter 3) and larger herbivores, such as pigs and deer, are only occasionally found within the wetland (Bishop C, 2013, pers. comm.). The importance of herbivory and seed predation is consistent with previous work in New Zealand: herbivory and seed predation have been found to affect the trajectory of successions, where palatable species are disproportionately targeted by herbivores (Wilson *et al.* 2006), or stall successions. Stalled (or arrested) successions (Young, Chase & Huddleston 2001) have been defined as an ecosystem state that has undergone compositional or structural change from the original ecosystem, and is trapped in a basin of attraction such that external intervention is required to resume the trajectory to the original ecosystem (Ghazoul *et al.* 2015). Stalled successions have been found using field surveys (Richardson, Holdaway & Carswell 2014) and spatial modelling approaches (Perry *et al.* 2015). Whether dispersal and biotic constraints have combined to stall succession within Awarua is discussed in Chapter 7, in light of this chapter and the spatial model of regeneration at the landscape level (Chapter 6).

Competition is relatively less important to forest regeneration, as clearing the understorey had no significant negative or positive effects on seedling establishment in the sowing experiment. This indicates there are available microsites within the wetland into which forest species, if dispersed and not eaten, may grow. However, invasive pest plant species (*Ulex europaeus*, *Rubus fruticosus*) are present within the wetland and have been documented as community invaders. The wetland is vulnerable to invasion in the period following fire, when mānuka is yet to establish, and as mānuka ages and senesces and allows sufficient light for establishment. *Ulex europaeus* increases the risk of subsequent fires due to its flammability (Perry, Wilmshurst & McGlone 2014). In addition to plots with *U. europaeus* identified in the vegetation survey, I observed *U. europaeus* around the edges of the wetland (including dense areas around the Craws Creek site), indicating seed sources exist to facilitate potential invasions.

The facilitative effect of the mānuka is documented as increasing as it ages (Burrows 1973; Esler & Astridge 1974), and consistent with this, I found that the experimentally thinned mānuka plots significantly improved seedling

survival and growth. The life span of mānuka has been estimated at 30-40 to 200 years (Burrows 1973). Given the average age of mānuka at Awarua (mean age 31 years), it is likely to become a more effective nurse species as it ages and self-thins, providing fire is excluded. Semi-open canopy mapped canopy types did have a higher canopy openness, but were overtaken by thinned canopy types in terms of seedling biomass. This suggests that waiting for areas mapped as dense mānuka to naturally thin out might provide a better environment than selecting areas currently mapped as semi-open.

Abiotic constraints

Based on the abiotic variables measured, I was able to extrapolate that all the sites were relatively similar in their abiotic suitability for forest. I confirmed this finding experimentally by sowing seeds at the two low-dispersal sites and found that seedlings established in all caged plots.

Although abiotic constraints or filters do not entirely prevent forest from establishing, it is unsurprising they affect the speed at which seedlings grow. The wetland is relatively acidic, and seedlings survived and grew best in the less acidic sites. This was particularly the case in the dense and thinned canopy types. Given the other differences in the semi-open canopy types (shorter, more open mānuka), it is likely factors other than pH are limiting seedling survival and growth, such as depth to groundwater. Depth to groundwater was included in the second best candidate model for sown seedling survival, after pH – see Appendix 2.7. Drier areas (increased depth to groundwater) were associated with better seedling survival (Appendix 2.7). The positive effect of drier areas is consistent with the results of the planting experiment under two nurse species (mānuka and *Chionochloa rubra*), which is discussed in Chapter 5.

Synthesis

Across all the experiments, it was apparent that the wetland is seed limited at multiple scales. Even where seed sources are nearby, dispersal limitation is filtering how many available seeds make it to suitable microsites. When seeds do arrive, biotic considerations of competition and facilitation are less important

than herbivory and predation, which were more important than environmental variables in both my univariate and multivariate analyses of seedling success.

Implications for restoration

At 20,000 ha, it is economically unviable to attempt to restore all of the wetland. One option is applied nucleation, in which clumps or 'nuclei' of vegetation are established to both 'catch' wind-blown seeds and attract bird dispersers (McDonnell & Stiles 1983; Guevara & Laborde 1993; Slocum 2001; Franks 2003). Forest is expected to regenerate from under and around these nuclei (Corbin & Holl 2012). However, increasing seed dispersal by itself is unlikely to be sufficient. Herbivory and seed predation not only decreased the net seedling survival and biomass, they also appeared to be influencing the trajectory of succession, with lower species and richness, and some species disproportionately affected by being uncaged. This is consistent with studies on the effects of herbivory on plant communities (Wardle *et al.* 2001) and succession (Coomes *et al.* 2003).

The mānuka is unlikely to senesce and self-thin for another sixty years, during which time the wetland is subject to switching to an alternative stable state (Suding, Gross & Houseman 2004; Hobbs, Higgs & Harris 2009): it remains in a highly flammable state, vulnerable to fire. There are seed sources of invasive shrub species around the wetland, which would have an opportunity to invade should a fire occur or while vacant niches are not filled by later successional native species. Forest regeneration trajectories differ between native and invasive exotic canopies (Sullivan, Williams & Timmins 2007), and are considered more likely to facilitate a second generation of exotic species (Sullivan, Williams & Timmins 2007). Invasive shrub species such as *Ulex europaeus* are highly flammable (Baeza *et al.* 2002), do not rely on bird dispersal (Moss 1959), have persistent seed banks (Partridge 1989; Hill, Gourlay & Barker 2001) and would make the wetland even more vulnerable to fire and a potential to become trapped in a highly flammable alternative stable state, in which fire begets another generation of *U. europaeus* (Perry *et al.* 2015).

Whether active restoration is advisable depends on the likelihood of natural regeneration, and the desired speed of regeneration relative to the cost and effectiveness of fire prevention and control. Given the interacting and potentially synergistic effect of the constraints discussed above and the vulnerable, flammable current state of the wetland, it is considered the wetland is a worthwhile candidate for active restoration efforts. Seed or seedling addition in drier, less acidic areas would address the seed and dispersal limitation found in the seed sowing experiment, vegetation survey and seed trapping experiment. In time, these planted areas would provide fruiting seed sources to attract birds to the wetland, and disperse seed within it. Planting efforts would be complemented by exclusion or control of exotic mammals that are likely to reduce the survival and growth of seedlings, and slow regeneration. Regeneration within the wetland is not impossible without active restoration efforts, but assistance would make the return of a mosaic of forest, mānuka and wetland species more likely, and more rapid, increasing the proportion of less flammable native species and reduce the system's vulnerability to fire.

Appendix 2.1 – Species list

Table 2.5: Species list of species found in vegetation survey at four sites within Awarua wetland in April 2012. Family, bio status, plant type and growth form data sourced from the NVS (National Vegetation Survey) database (Wiser, Bellingham & Burrows 2001)

Family	Species	Bio status	Plant type	Growth form
Cyperaceae	*Carex appressa*	Indigenous Non-Endemic	Vascular	Graminoid
Cyperaceae	*Carex* species	Indigenous Non-Endemic	Vascular	Graminoid
Rousseaceae	*Carpodetus serratus*	Indigenous Endemic	Vascular	Tree
Gramineae	*Chionochloa rubra*	Indigenous Endemic	Vascular	Graminoid
Rubiaceae	*Coprosma ciliata*	Indigenous Endemic	Vascular	Shrub
Rubiaceae	*Coprosma foetidissima*	Indigenous Endemic	Vascular	Tree
Rubiaceae	*Coprosma linariifolia*	Indigenous Endemic	Vascular	Tree
Rubiaceae	*Coprosma microcarpa*	Indigenous Endemic	Vascular	Shrub
Rubiaceae	*Coprosma propinqua*	Indigenous Endemic	Vascular	Tree
Rubiaceae	*Coprosma rhamnoides*	Indigenous Endemic	Vascular	Shrub
Rubiaceae	*Coprosma tayloriae*	Indigenous Endemic	Vascular	Tree
Ericaceae	*Cyathodes acerosa*	Indigenous Non-Endemic	Vascular	Shrub
Ericaceae	*Dracophyllum longifolium*	Indigenous Endemic	Vascular	Tree
Elaeocarpaceae	*Elaeocarpus hookerianus*	Indigenous Endemic	Vascular	Tree
Restionaceae	*Empodisma minus*	Indigenous Non-Endemic	Vascular	Graminoid
Ericaceae	*Gaultheria crassa*	Indigenous Endemic	Vascular	Shrub
Gleicheniaceae	*Gleichenia dicarpa*	Indigenous Non-Endemic	Vascular	Fern
Griseliniaceae	*Griselinia littoralis*	Indigenous Endemic	Vascular	Tree
Dennstaedtiaceae	*Histiopteris incisa*	Indigenous Non-Endemic	Vascular	Fern
Cyperaceae	*Isolepis species*	Indigenous Non-Endemic	Vascular	Graminoid

Juncaceae	*Juncus species*	Indigenous Non-Endemic	Vascular	Graminoid
Myrtaceae	*Leptospermum scoparium*	Indigenous Non-Endemic	Vascular	Tree
Ericaceae	*Leucopogon fasciculatus*	Indigenous Endemic	Vascular	Shrub
NA	Moss	Indigenous Non-Endemic	Non Vascular	NonVascular
NA	Other fern	NA	Vascular	Fern
Hemerocallidaceae	*Phormium tenax*	Indigenous Endemic	Vascular	Graminoid
Podocarpaceae	*Phyllocladus alpinus*	Indigenous Endemic	Vascular	Tree
Pittosporaceae	*Pittosporum tenuifolium*	Indigenous Endemic	Vascular	Tree
Gramineae	Poa species	Indigenous Non-Endemic	Vascular	Graminoid
Podocarpaceae	*Podocarpus cunninghamii*	Indigenous Endemic	Vascular	Tree
Araliaceae	*Pseudopanax crassifolius*	Indigenous Endemic	Vascular	Tree
Dennstaedtiaceae	*Pteridium esculentum*	Indigenous Non-Endemic	Vascular	Fern
Araliaceae	*Raukaua simplex*	Indigenous Endemic	Vascular	Tree
Rosaceae	*Rubus fruticosus*	Exotic	Vascular	SubShrub
Sphagnaceae	Sphagnum species	Indigenous Non-Endemic	Non Vascular	NonVascular
Leguminosae	*Ulex europaeus*	Exotic	Vascular	Shrub

Appendix 2.2: Vegetation survey – species differing in cover between sites

Table 2.7: Species which vary significantly in their average plot cover between sites: (a) Average mean cover per plot (%); (b) Significance (unadjusted and adjusted for multiple comparisons presented); (c) the percentage of plots which contain the species. Full species names are: *Gleichena dicarpa, Empodisma minus, Leptospermum scoparium, Coprosma ciliata, Griselinia littoralis, Pittosporum tenuifolium, Pseudopanax crassifolius, Rubus fruticosus, Ulex europaeus*

	(a) Average mean ground cover per plot (%)				(b) Significance		(c) Percentage of plots - presence			
	Craws Creek	Lawsons	Clearwater	Tiwai	p unadj	p adj	Craws Creek	Lawsons	Clearwater	Tiwai
G. dicarpa	1.41	5.55	4	6.67	0.038	0.393	10	25	27.5	30
E. minus	1.21	4.02	7.39	13.98	0.002	0.02	7.5	30	32.5	72.5
L. scoparium	84.52	89.18	91.58	88.73	0.027	0.107	100	100	100	100
C. ciliata	1.73	1.52	0.05	0	0.01	0.081	20	25	2.5	0
Sphagnum species	4.34	0	4.29	0	0.002	0.002	17.5	0	22.5	0
G. littoralis	8.59	1.85	0	0	0.001	0.001	72.5	32.5	0	0
P. tenuifolium	8.14	0.86	0	0	0.001	0.005	60	12.5	0	0
P. crassifolius	3.06	0.08	0.08	0	0.002	0.118	35	2.5	2.5	0
R. fruticosus	0	0	0	1.23	0.025	0.375	0	0	0	15
U. europeaus	0	0	0.86	3.37	0.042	0.501	0	0	2.5	15

Appendix 2.3: Vegetation survey – regeneration cover

Table 2.7: Amount of regeneration by site within Awarua. Each site contained 40 plots. Number of plots is the number of plots at each site that contained native forest species. Mean count is the mean number of forest seedlings or trees found within each plot. Mean cover is the mean cover (%) of forest species within each plot. Mean total height is the mean total height of all seedlings and trees within each plot, binned to the nearest ten cm for seedlings under 1 m.

Site	Plots with regen	Seedlingsper plot	se count	Forest species cover (%)	se cover	Mean total height (cm)	se height
Craws Creek	33	14.88	3.06	10.77	3.53	484.13	133.41
Lawsons	17	1.33	0.36	0.54	0.31	21.63	7.17
Clearwater	6	0.68	0.40	2.33	1.39	64.15	35.27
Tiwai	1	0.00	0.00	0.78	0.78	0.00	0.00

Appendix 2.4: Seed sowing experiment – seedling survival model summary

Table 2.8: Model coefficients for seedling survival in the seed sowing experiment. Seedling survival is the number of seedlings surviving per replicate out of the number sown (140). I present the full model (additive effects of canopy type, understorey clearance and caging, and all interactions thereof), and the best reduced model. I tested for the best model by comparing all possible subsets of the full model using the Information-Theoretic Model Comparison approach (Burnham & Anderson 2002). Canopy SO = semi-open canopy, canopy TH = thinned canopy, caging UC = uncaged treatment, understorey UNCL = uncleared understorey.

Full model

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-1.99209	0.1943	-10.252	0.000	***
Canopy SO	0.3921	0.27108	1.446	0.1481	
Canopy TH	0.51131	0.27005	1.893	0.0583	.
Understorey UNCL	-0.12931	0.26575	-0.487	0.6266	
Caging UC	-1.2444	0.29353	-4.239	0.000	***
Canopy SO:Understorey UNCL	0.09156	0.36943	0.248	0.8043	
Canopy TH:Understorey UNCL	0.055	0.36803	0.149	0.8812	
Canopy SO:Caging UC	0.60193	0.39431	1.527	0.1269	
Canopy TH:Caging UC	-0.18671	0.40282	-0.464	0.643	
Understorey UNCL:Caging UC	0.23551	0.41162	0.572	0.5672	
Canopy SO:Understorey UNCL:Caging UC	-0.3428	0.55704	-0.615	0.5383	
Canopy TH:Understorey UNCL:Caging UC	0.315	0.56342	0.559	0.5761	

Reduced model

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-2.1227	0.1266	-16.766	0.000	***
Canopy SO	0.6375	0.1599	3.987	0.000	***
Canopy TH	0.5311	0.1603	3.314	0.000	***
Caging UC	-0.9854	0.119	-8.282	0.000	***

Appendix 2.5: Seed sowing experiment – seedling biomass model summary

Table 2.9: Model coefficients for biomass (summed seedling height per replicate in cm) in the seed sowing experiment. Biomass was square-root transformed. I present the full model (additive effects of canopy type, understorey clearance and caging, and all interactions thereof), and the best reduced model. I tested for the best model by comparing all possible subsets of the full model using the Information-Theoretic Model Comparison approach (Burnham & Anderson 2002). Canopy SO = semi-open canopy, canopy TH = thinned canopy, caging UC = uncaged treatment, understorey UNCL = uncleared understorey.

Full model

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	7.565	0.72	10.49	0.000	***
Canopy SO	0.853	1.02	0.84	0.403	
Canopy TH	2.162	1.02	2.12	0.034	*
Understorey UNCL	-0.273	0.90	-0.30	0.761	
Caging UC	-3.968	0.90	-4.42	0.000	***
Canopy SO:Understorey UNCL	0.889	1.27	0.70	0.484	
Canopy TH:Understorey UNCL	0.575	1.27	0.45	0.651	
Canopy SO:Caging UC	1.697	1.27	1.34	0.182	
Canopy TH:Caging UC	-1.274	1.27	-1.00	0.316	
Understorey UNCL:Caging UC	0.574	1.27	0.45	0.652	
Canopy SO:Understorey UNCL:Caging UC	-1.044	1.80	-0.58	0.561	
Canopy TH:Understorey UNCL:Caging UC	0.948	1.80	0.53	0.598	

Reduced model

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	7.429	0.57	13.07	0.000	***
Canopy SO	1.297	0.80	1.61	0.107	
Canopy TH	2.449	0.80	3.05	0.002	**
Caging UC	-3.681	0.65	-5.64	0.000	***
Canopy SO:Understorey UNCL	1.175	0.92	1.27	0.203	
Canopy TH:Understorey UNCL	-0.800	0.92	-0.87	0.386	

Appendix 2.6: Seed sowing experiment – species-specific seedling survival model summary

Table 2.10: Species-specific seedling survival results. Response is the number of seedlings surviving as a proportion of the number sown. The model models the proportion of seedlings surviving per replicate and for each species as a response to the species + species:caging + species:canopy. Codes are (in order of appearance in table): GL = *G. littoralis*. ML= *M. lanceolatus*, PT = *Pittosporum tenuifolium*, RS = *Raukaua simplex*, PC = *Pseudopanax crassifolius*, SO = semi-open canopy, TH = thinned canopy, UC = uncaged.

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-0.24658	0.33719	-0.731	0.464617	
GL	-4.13449	0.58112	-7.115	1.12E-12	***
ML	-3.61468	0.5715	-6.325	2.53E-10	***
PT	-1.36497	0.49331	-2.767	0.005658	**
RS	-1.39535	0.46811	-2.981	0.002875	**
PC:SO	0.26979	0.47593	0.567	0.570794	
GL:SO	1.4009	0.62663	2.236	0.025376	*
ML:SO	0.40154	0.66142	0.607	0.543793	
PT:SO	0.99725	0.53182	1.875	0.060772	.
RS:SO	1.07028	0.49318	2.17	0.029994	*
PC:TH	0.79499	0.47757	1.665	0.095984	.
GL:TH	1.0919	0.63662	1.715	0.086317	.
ML:TH	0.84065	0.63608	1.322	0.186295	
PT:TH	1.29139	0.53278	2.424	0.015355	*
RS:TH	0.6591	0.49769	1.324	0.185392	
PC:UC	-1.64978	0.49767	-3.315	0.000916	***
GL:UC	-1.53744	0.95423	-1.611	0.107142	
ML:UC	-1.26954	0.85654	-1.482	0.138295	
PT:UC	-1.4562	0.62676	-2.323	0.02016	*
RS:UC	-0.77002	0.52177	-1.476	0.14	
PC:SO:UC	0.76825	0.69079	1.112	0.266082	
GL:SO:UC	0.57409	1.11993	0.513	0.608221	
ML:SO:UC	-0.63246	1.24379	-0.508	0.611108	
PT:SO:UC	-0.07806	0.8308	-0.094	0.925143	
RS:SO:UC	0.03032	0.71246	0.043	0.966051	
PC:TH:UC	-0.22543	0.69587	-0.324	0.745969	
GL:TH:UC	0.28596	1.15759	0.247	0.804884	
ML:TH:UC	-0.34983	1.12729	-0.31	0.756312	
PT:TH:UC	-0.17401	0.83038	-0.21	0.834014	
RS:TH:UC	-0.08498	0.72056	-0.118	0.90612	

Appendix 2.7: Model selection, seedling survival & abiotic variables

Data & packages

```
require(lme4)
require(MuMIn)

febsownsurvival2 <- read.csv("modelsel_survival.csv")
```

Set of candidate models

```
Cand.models <- list()

# The first model is the maximal model
Cand.models[[1]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ can
opy +
                            caging + understorey +
                            canopy:caging +
                            caging:understorey +
                            canopy:caging:understorey +
                            pH + log_co +
                            log_co:canopy +
                            total.N  + log_P +
                            log_height +
                            log_height:caging +
                            log_height:canopy +
                            log_age + log_age:canopy +
                            log_water:log_co +
                            log_water:log_co:log_height +
                            log_water +
                            (1|site/canopy/understorey/caging) + (1|obs),
                          family = "binomial",
                          na.action = "na.fail",
                          data = febsownsurvival2)

# Second model is the NULL model (random effects only)
Cand.models[[2]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~(1|s
ite/canopy/understorey/caging)+ (1|obs),
                          family = "binomial",
                          na.action = "na.fail",
                          data = febsownsurvival2)

Cand.models[[3]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ log
```

```
_height + (1|site/canopy/understorey/caging)+ (1|obs),
                          family = "binomial",
                          na.action = "na.fail",
                          data = febsownsurvival2)

Cand.models[[4]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ tot
al.N + (1|site/canopy/understorey/caging)+ (1|obs),
                          family = "binomial",
                          na.action = "na.fail",
                          data = febsownsurvival2)

Cand.models[[5]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ log
_P + (1|site/canopy/understorey/caging)+ (1|obs),
                          family = "binomial",
                          na.action = "na.fail",
                          data = febsownsurvival2)

Cand.models[[6]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ log
_co + (1|site/canopy/understorey/caging)+ (1|obs),
                          family = "binomial",
                          na.action = "na.fail",
                          data = febsownsurvival2)

Cand.models[[7]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ log
_co + canopy + caging + log_co:log_water + (1|site/canopy/understorey/caging)
+ (1|obs),
                          family = "binomial",
                          na.action = "na.fail",
                          data = febsownsurvival2)

Cand.models[[8]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ log
_water + (1|site/canopy/understorey/caging)+ (1|obs),
                          family = "binomial",
                          na.action = "na.fail",
                          data = febsownsurvival2)

Cand.models[[9]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ log
_age + (1|site/canopy/understorey/caging)+ (1|obs),
                          family = "binomial",
                          na.action = "na.fail",
                          data = febsownsurvival2)

Cand.models[[10]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
ging + (1|site/canopy/understorey/caging)+ (1|obs),
                           family = "binomial",
                           na.action = "na.fail",
                           data = febsownsurvival2)

Cand.models[[11]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
```

```
nopy + (1|site/canopy/understorey/caging)+ (1|obs),
                           family = "binomial",
                           na.action = "na.fail",
                           data = febsownsurvival2)

Cand.models[[12]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ un
derstorey + (1|site/canopy/understorey/caging)+ (1|obs),
                           family = "binomial",
                           na.action = "na.fail",
                           data = febsownsurvival2)

Cand.models[[13]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
ging + canopy +
                             (1|site/canopy/understorey/caging)+ (1|obs),
                           family = "binomial",
                           na.action = "na.fail",
                           data = febsownsurvival2)

Cand.models[[14]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
ging + canopy + caging:canopy +
                             (1|site/canopy/understorey/caging)+ (1|obs),
                           family = "binomial",
                           na.action = "na.fail",
                           data = febsownsurvival2)

Cand.models[[15]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
ging * canopy * understorey +
                             (1|site/canopy/understorey/caging)+ (1|obs),
                           family = "binomial",
                           na.action = "na.fail",
                           data = febsownsurvival2)

Cand.models[[16]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
ging * canopy + understorey +
                             (1|site/canopy/understorey/caging)+ (1|obs),
                           family = "binomial",
                           na.action = "na.fail",
                           data = febsownsurvival2)

Cand.models[[17]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
ging + canopy + understorey +
                             (1|site/canopy/understorey/caging)+ (1|obs),
                           family = "binomial",
                           na.action = "na.fail",
                           data = febsownsurvival2)

# Based on modelling of fixed effects, including fixed effects and interactio
ns with environmental variables
```

```r
# canopy openness
Cand.models[[18]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
ging * canopy + log_co + canopy:log_co +
                            (1|site/canopy/understorey/caging)+ (1|obs),
                          family = "binomial",
                          na.action = "na.fail",
                          data = febsownsurvival2)

# depth to water table
Cand.models[[19]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
ging * canopy + log_water + canopy:log_water +
                            (1|site/canopy/understorey/caging)+ (1|obs),
                          family = "binomial",
                          na.action = "na.fail",
                          data = febsownsurvival2)

# pH
Cand.models[[20]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
ging * canopy + pH + canopy:pH +
                            (1|site/canopy/understorey/caging)+ (1|obs),
                          family = "binomial",
                          na.action = "na.fail",
                          data = febsownsurvival2)

# pH no interaction
Cand.models[[21]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
ging * canopy + pH +
                            (1|site/canopy/understorey/caging)+ (1|obs),
                          family = "binomial",
                          na.action = "na.fail",
                          data = febsownsurvival2)

# CO no interaction
Cand.models[[22]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
ging * canopy + log_co +
                            (1|site/canopy/understorey/caging)+ (1|obs),
                          family = "binomial",
                          na.action = "na.fail",
                          data = febsownsurvival2)

# GW no interaction
Cand.models[[23]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
ging * canopy + log_water +
                            (1|site/canopy/understorey/caging)+ (1|obs),
                          family = "binomial",
                          na.action = "na.fail",
                          data = febsownsurvival2)

# CH
```

```
Cand.models[[24]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
ging * canopy + log_height + log_height:canopy +
                            (1|site/canopy/understorey/caging)+ (1|obs),
                          family = "binomial",
                          na.action = "na.fail",
                          data = febsownsurvival2)

# CH no interaction
Cand.models[[25]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
ging * canopy + log_height + (1|site/canopy/understorey/caging)+ (1|obs),
                          family = "binomial",
                          na.action = "na.fail",
                          data = febsownsurvival2)

# CH + CO
Cand.models[[26]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
ging + canopy + caging:canopy + log_height + log_co   +
                            (1|site/canopy/understorey/caging)+ (1|obs),
                          family = "binomial",
                          na.action = "na.fail",
                          data = febsownsurvival2)

# CH + CO + CO interaction
Cand.models[[27]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
ging + canopy + caging:canopy + log_height + log_co  + log_co:canopy  +
                            (1|site/canopy/understorey/caging)+ (1|obs),
                          family = "binomial",
                          na.action = "na.fail",
                          data = febsownsurvival2)

# soil nutrient status - N and P
Cand.models[[28]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
ging * canopy + total.N + log_P +
                            (1|site/canopy/understorey/caging)+ (1|obs),
                          family = "binomial",
                          na.action = "na.fail",
                          data = febsownsurvival2)

# N + P plus interactions
Cand.models[[29]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
ging * canopy + total.N + log_P + canopy:total.N + canopy:log_P +
                            (1|site/canopy/understorey/caging)+ (1|obs),
                          family = "binomial",
                          na.action = "na.fail",
                          data = febsownsurvival2)

# CH, CO, canopy interaction
Cand.models[[30]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
ging + canopy + log_height + log_co +
```

```
                              caging:canopy + canopy:log_height + canopy:log_c
o + canopy:log_co:log_height + (1|site/canopy/understorey/caging)+ (1|obs),
                            family = "binomial",
                            na.action = "na.fail",
                            data = febsownsurvival2)

# N  plus interaction
Cand.models[[31]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
ging * canopy + total.N + canopy:total.N  +  (1|site/canopy/understorey/cagin
g)+ (1|obs),
                            family = "binomial",
                            na.action = "na.fail",
                            data = febsownsurvival2)

# P  plus interaction
Cand.models[[32]] <- glmer(cbind(count_seedlings, 140 - count_seedlings) ~ ca
ging * canopy  + log_P + log_P:canopy+  (1|site/canopy/understorey/caging)+ (
1|obs),
                            family = "binomial",
                            na.action = "na.fail",
                            data = febsownsurvival2)
```

Model selection table

```
model.sel.out <- model.sel(Cand.models)

print(subset(model.sel.out, delta < 4), row.names = FALSE)
```

```
## Model selection table
##     (Int) cgn cnp log_wtr     pH   ttl.N cgn:cnp cnp:pH cnp:ttl.N df
## 20 -5.492   +   +         0.8127               +      +           14
## 31 -1.387   +   +                -0.4485       +                + 14
## 21 -3.560   +   +         0.3555               +                  12
## 13 -2.123   +   +                                                   9
## 23 -3.041   +   +  0.2939                      +                  12
##      logLik  AICc delta weight
## 20 -316.723 666.6  0.00  0.430
## 31 -317.458 668.1  1.47  0.206
## 21 -320.288 668.3  1.70  0.184
## 13 -324.815 669.7  3.09  0.092
## 23 -321.021 669.8  3.17  0.088
## Models ranked by AICc(x)
## Random terms (all models):
## '1 | site/canopy/understorey/caging', '1 | obs'
```

Summary of best model

```
# model 20 was the best model
coefficients_20 <- data.frame(summary(Cand.models[[20]])$coefficients)
coefficients_20$variable <- row.names(coefficients_20)
row.names(coefficients_20) <- NULL
names(coefficients_20) <- c("Estimate", "SE", "z_value", "P", "Variable")
coefficients_20 <- coefficients_20[ , c(5, 1, 2, 3, 4)]

coefficients_20$Estimate <- round(coefficients_20$Estimate, 2)
coefficients_20$SE <- round(coefficients_20$SE, 2)
coefficients_20$z_value <- round(coefficients_20$z_value, 2)
coefficients_20$P <- round(coefficients_20$P, 3)

print(coefficients_20, row.names = FALSE)
```

```
##                      Variable Estimate   SE z_value     P
##                   (Intercept)    -5.49 1.03   -5.32 0.000
##                  caginguncaged    -1.17 0.20   -5.70 0.000
##                 canopysemiopen     4.36 1.47    2.97 0.003
##                  canopythinned     2.52 1.49    1.70 0.090
##                             pH     0.81 0.24    3.36 0.001
##  caginguncaged:canopysemiopen     0.47 0.27    1.73 0.084
##   caginguncaged:canopythinned     0.03 0.28    0.09 0.925
##              canopysemiopen:pH    -0.92 0.34   -2.72 0.007
##               canopythinned:pH    -0.47 0.35   -1.37 0.172
```

Appendix 2.8: Model selection, seedling biomass & abiotic variables

Data & packages

```
require(lme4)
require(MuMIn)
require(glmmADMB)

febsowngrowthall_env <- read.csv("modelsel_heights.csv")
```

Set of candidate models

```
Cand.models.height <- list()

# The first model is the maximal model
Cand.models.height[[1]] <- lmer(sqrt_plotheight ~ canopy +  caging +
                                  understorey + canopy:caging +
                                  canopy:understorey +
                                  canopy:caging:understorey +
                                  pH + log_co +
                                  log_co:canopy +
                                  total.N + log_P +
                                  log_height +
                                  log_height:caging +
                                  log_height:canopy +
                                  log_age +
                                  log_age:canopy +
                                  log_water:log_co +
                                  log_water:log_co:log_height +
                                  log_water +
                                  (1|site/canopy/understorey/caging),
                                na.action = "na.fail",
                                data = febsowngrowthall_env)

# Second model is the null model (random effects only)

Cand.models.height[[2]] <- lmer(sqrt_plotheight
~(1|site/canopy/understorey/caging),
                                na.action = "na.fail",
                                data = febsowngrowthall_env)

# Single factor treatments
```

```
Cand.models.height[[3]] <- lmer(sqrt_plotheight ~ log_height +
(1|site/canopy/understorey/caging),
                                na.action = "na.fail",
                                data = febsowngrowthall_env)

Cand.models.height[[4]] <- lmer(sqrt_plotheight ~ total.N +
(1|site/canopy/understorey/caging),
                                na.action = "na.fail",
                                data = febsowngrowthall_env)

Cand.models.height[[5]] <- lmer(sqrt_plotheight ~ log_P +
(1|site/canopy/understorey/caging),
                                na.action = "na.fail",
                                data = febsowngrowthall_env)

Cand.models.height[[6]] <- lmer(sqrt_plotheight ~ log_co +
(1|site/canopy/understorey/caging),
                                na.action = "na.fail",
                                data = febsowngrowthall_env)

Cand.models.height[[7]] <- lmer(sqrt_plotheight ~ log_co + canopy +
caging + log_co:log_water + (1|site/canopy/understorey/caging),
                                na.action = "na.fail",
                                data = febsowngrowthall_env)

Cand.models.height[[8]] <- lmer(sqrt_plotheight ~ log_water +
(1|site/canopy/understorey/caging),
                                na.action = "na.fail",
                                data = febsowngrowthall_env)

Cand.models.height[[9]] <- lmer(sqrt_plotheight ~ log_age +
(1|site/canopy/understorey/caging),
                                na.action = "na.fail",
                                data = febsowngrowthall_env)

Cand.models.height[[10]] <- lmer(sqrt_plotheight ~ caging +
(1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)

Cand.models.height[[11]] <- lmer(sqrt_plotheight ~ canopy +
(1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)

Cand.models.height[[12]] <- lmer(sqrt_plotheight ~ understorey +
(1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)
```

```
# Interaction factor treatments

Cand.models.height[[13]] <- lmer(sqrt_plotheight ~ caging + canopy +
(1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)


Cand.models.height[[14]] <- lmer(sqrt_plotheight ~ caging + canopy +
caging:canopy + (1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)

Cand.models.height[[15]] <- lmer(sqrt_plotheight ~ caging * canopy *
understorey + (1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)

Cand.models.height[[16]] <- lmer(sqrt_plotheight ~ caging * canopy +
understorey + (1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)


Cand.models.height[[17]] <- lmer(sqrt_plotheight ~ caging + canopy +
understorey + (1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)


# Based on modelling of fixed effects, including fixed effects and
interactions with environmental variables


# canopy openness
Cand.models.height[[18]] <- lmer(sqrt_plotheight ~ caging * canopy +
log_co + canopy:log_co + (1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)

# depth to water table
Cand.models.height[[19]] <- lmer(sqrt_plotheight ~ caging * canopy +
log_water + canopy:log_water + (1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)
```

```r
# pH
Cand.models.height[[20]] <- lmer(sqrt_plotheight ~ caging * canopy + pH
+ canopy:pH + (1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)

# pH no interaction
Cand.models.height[[21]] <- lmer(sqrt_plotheight ~ caging * canopy + pH
+ (1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)

# CO no interaction
Cand.models.height[[22]] <- lmer(sqrt_plotheight ~ caging * canopy +
log_co + (1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)

# GW no interaction
Cand.models.height[[23]] <- lmer(sqrt_plotheight ~ caging * canopy +
log_water + (1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)

# CH
Cand.models.height[[24]] <- lmer(sqrt_plotheight ~ caging * canopy +
log_height + log_height:canopy + (1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)

# CH no interaction
Cand.models.height[[25]] <- lmer(sqrt_plotheight ~ caging * canopy +
log_height + (1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)

# CH + CO
Cand.models.height[[26]] <- lmer(sqrt_plotheight ~ caging + canopy +
caging:canopy + log_height + log_co   +
(1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)

# CH + CO + CO interaction
Cand.models.height[[27]] <- lmer(sqrt_plotheight ~ caging + canopy +
caging:canopy + log_height + log_co  + log_co:canopy  +
(1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)
```

```
# soil nutrient status - N and P
Cand.models.height[[28]] <- lmer(sqrt_plotheight ~ caging * canopy +
total.N + log_P + (1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)

# N + P plus interactions
Cand.models.height[[29]] <- lmer(sqrt_plotheight ~ caging * canopy +
total.N + log_P + canopy:total.N + canopy:log_P +
(1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)

# CH, CO, canopy interaction

Cand.models.height[[30]] <- lmer(sqrt_plotheight ~ caging + canopy +
log_height + log_co +
                                   caging:canopy + canopy:log_height +
canopy:log_co + canopy:log_co:log_height +
                                   (1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)


# N  plus interaction

Cand.models.height[[31]] <- lmer(sqrt_plotheight ~ caging * canopy +
total.N + canopy:total.N  +  (1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)


# P  plus interaction

Cand.models.height[[32]] <- lmer(sqrt_plotheight ~ caging * canopy  +
log_P + log_P:canopy+  (1|site/canopy/understorey/caging),
                                 na.action = "na.fail",
                                 data = febsowngrowthall_env)
```

Model selection table

```
model.sel.out.heights <- model.sel(Cand.models.height)
print(subset(model.sel.out.heights, delta < 4), row.names = FALSE)

## Model selection table
##     (Int) cgn cnp log_co log_hgh    pH cgn:cnp cnp:log_co
```

```
cnp:log_hgh
## 20 -6.478   +   +                3.294       +
## 30  5.117   +   +   7.27  0.6395              +          +
+
##    cnp:pH cnp:log_co:log_hgh df   logLik  AICc delta weight
## 20      +                    14 -182.159 397.5  0.00  0.774
## 30                         + 20 -174.381 400.0  2.46  0.226
## Models ranked by AICc(x)
## Random terms (all models):
## '1 | site/canopy/understorey/caging'
```

Summary of best model

```
# model 20 was the best model
# using glmmadmb for p values

model_20_heights <- glmmadmb(sqrt_plotheight ~ caging * canopy + pH +
canopy:pH +
                               (1 | site/canopy/understorey/caging),
                             family = "gaussian",
                             data = febsowngrowthall_env)

coefficients_20_heights <-
data.frame(summary(model_20_heights)$coefficients)
coefficients_20_heights$variable <- row.names(coefficients_20_heights)
row.names(coefficients_20_heights) <- NULL
names(coefficients_20_heights) <- c("Estimate", "SE", "z_value", "P",
"Variable")
coefficients_20_heights <- coefficients_20_heights[ , c(5, 1, 2, 3, 4)]
coefficients_20_heights$Estimate <-
round(coefficients_20_heights$Estimate, 2)
coefficients_20_heights$SE <- round(coefficients_20_heights$SE, 2)
coefficients_20_heights$z_value <-
round(coefficients_20_heights$z_value, 2)
coefficients_20_heights$P <- round(coefficients_20_heights$P, 3)

print(coefficients_20_heights, row.names = FALSE)
```

```
##                      Variable Estimate   SE z_value     P
##                   (Intercept)    -6.59 3.16   -2.09 0.037
##                 caginguncaged    -3.68 0.59   -6.29 0.000
##               canopysemiopen    15.08 4.66    3.24 0.001
##                canopythinned     5.03 4.69    1.07 0.283
##                           pH     3.32 0.74    4.48 0.000
##  caginguncaged:canopysemiopen     1.18 0.83    1.42 0.156
##   caginguncaged:canopythinned    -0.80 0.83   -0.97 0.334
##            canopysemiopen:pH    -3.27 1.08   -3.04 0.002
##             canopythinned:pH    -0.65 1.09   -0.60 0.551
```

Chapter Three: Monitoring duration and interspecies interference affect detection rates in chew cards

3.1 Foreword & declaration of contributions

This chapter has been submitted as a paper to *Austral Ecology*, and is currently under review at the time of thesis submission. Aside from minor formatting changes, it is presented as submitted and retains the pronoun 'we' as my supervisors Prof. Dave Kelly and Assoc. Prof. Janet Wilmshurst are co-authors on the paper. I (Olivia Burge) designed the experiment, undertook the fieldwork, analysed the data and wrote the first, second and final drafts of the paper. DK and JW reviewed the first and second drafts of the paper.

3.2 Abstract

Pest monitoring methods should provide unbiased accurate estimates of pest densities and locations, while also minimising time-in-field and costs. Recent pest monitoring studies have found chew cards are more effective than conventional monitoring methods, but little experimental work has been done to determine optimal experimental duration or quantify the risks of saturation by one species biasing detections of other species. Here we used chew cards in three sites within Awarua wetland (Southland, New Zealand) to investigate the amount of time required to detect target pest species (rats, possums and mice) at sufficient sensitivity, and to examine their potential to bias detection rates of other species. We found significantly depressed detections of possums and rats where a contraspecific (an animal of a different species) had been detected on a card, which is consistent with previous studies of a similar duration on interspecies interference. This experiment is the first to analyse the rates at which species accrue on transects by night, and we found rat detections lagged behind possums for the first four nights. We modelled the effect of duration and

rat detections on the likelihood of further possum detections on transects. Duration and rat detections interacted significantly, meaning there are trade-offs to be considered with regard to duration: shorter durations may avoid the risk of saturation in areas of high pest density, but risk not sampling neophobic populations. Our data suggest chew cards remain one of the most sensitive pest monitoring tools for rats and possums, compared to conventional methods such as tracking tunnels and wax tags. In areas of moderate pest densities, we suggest a duration of five nights is optimal for detecting pests with sufficient sensitivity. However, in areas of high pest density the sensitivity of chew cards may render them unsuitable because of significant saturation and interspecies interference effects.

3.3 Introduction

Wildlife monitoring for conservation or pest management requires knowledge of the location and abundance of the target species. Relative abundance indices are more commonly used than absolute abundance measures. The latter can be time- and cost- prohibitive where the study area is large, or multiple areas are monitored (Caughley 1977; Pendleton 1995; Pollock *et al.* 2002) and relative measures are sufficient for many research and management decisions (Caughley 1977; Skalski & Robson 1992). Monitoring methods are ideally sensitive, easy to interpret, and cost-effective to deploy (Sweetapple & Nugent 2011; Hutchings, Hancox & Livingstone 2013).

The validity of relative measures requires that there is a constant probability of detection based on a constant proportionality (Pendleton 1995; Ruscoe, Goldsmith & Choquenot 2001; Norvell, Howe & Parrish 2003). For example, this condition would be violated if detection likelihoods differed between habitats included within a study, where understorey growth differed in density and affected detection probabilities, or where equipment becomes 'saturated' by other abundant species. Standardised survey methods and conditions are designed to maintain the likelihood of consistent detection probability (Pendleton 1995). Conner, Labisky and Progulske (1983) note that standardising methods for relative abundance indices is a necessary but not sufficient

condition for comparisons between studies. Factors which lead to a violation of the assumption of constant probabilities of detection – such as differential detection rates in different habitats – will lead to a lack of robust comparisons, in this case between habitats (Conner, Labisky & Progulske 1983). However, while violation of the assumptions can invalidate comparisons between areas, they are less likely to affect comparisons within areas over time (assuming spatial factors remain the same).

In New Zealand, where forests and birdlife are affected by invasive species, only one-eighth of the conservation estate is actively managed for pest species control (Wright 2011). Advances in pest species monitoring complements advances in pest control methods such as 1080 application techniques (Nugent *et al.* 2010; Nugent *et al.* 2012) and other control methods (Thomas & Taylor 2002; Towns & Broome 2003; Howald *et al.* 2007). Cheaper and more effective monitoring will ultimately contribute to increasing the success and size of pest control programmes.

Historically various methods have been used for commonly monitored pest species in New Zealand - brushtail possums *(Trichosurus vulpecula*), rats (*Rattus* sp.) and mice (*Mus musculus*). Pickerell *et al.* (2014) recently reviewed pest monitoring methods in non-forested habitats and found that few of the currently available methods were able to detect key species with any reliability. However this review excluded any discussion of chew cards, which are small (90 x 180 mm) rectangular polypropylene sheets with baited flutes (Sweetapple and Nugent 2011). Species' presences on a chew card are determined by distinctive bite marks – the primary method – as well as track marks and DNA. Transects of cards are the typical unit of analysis, and relative abundance is expressed as the proportion of cards detecting a species per transect.

Faecal pellet counts were originally used to monitor possums in New Zealand (Baddeley 1985). By 1996 most monitoring had shifted to trap catch index (TCI), i.e. the percentage of leghold traps which catch possums over a three-night duration (Forsyth *et al.* 2005). This is a relatively costly measure, given the

frequency of visits required for ethical reasons (see Sweetapple and Nugent (2011)) and replication is limited due to the weight of traps (Thomas *et al.* 2003). The strongest correlation with radio-transmitter monitored catch-and-release estimates of density for possums comes from kill traps ($R^2 = 0.91$, Warburton *et al* (2004).

Scented paraffin wax lures ("wax tags") have been used to detect both possums and rodent species through identification of species-specific bite marks (Innes *et al.* 1995; Thomas 1999; Blackwell, Potter & McLennan 2002), and are a cheaper alternative to traps. Pickerell *et al.* (2014) found wax tags were the most efficient at detecting possums. However they are poor at detecting mice, are vulnerable to non-animal damage (Thomas 1999), and have a lower correlation with possum density than kill traps ($R^2 = 0.66$, Warburton, Barker and Coleman (2004)). In addition to wax tags, tracking tunnels are commonly used to monitor rodent species (Innes *et al.* 1995; Blackwell, Potter & McLennan 2002). Tracking tunnels contain bait and an inkpad surrounded by paper. Species-specific footprints (or 'tracks') allow identification of species presences and although bulkier than chew cards, allow relatively easy data collection (Ogilvie *et al.* 2006). There are standardised protocols for residual trap catch and wax tags for possums (NPCA 2010; NPCA 2011) and New Zealand Department of Conservation guidance for tracking tunnels (Gillies & Williams 2013).

Chew cards were developed as a lightweight alternative to detect multiple species (Sweetapple & Nugent 2011). Chew cards have been shown to be more sensitive than wax tags at detecting possums (Sweetapple & Nugent 2011) and more sensitive than tracking tunnels for rats (Ruffell, Innes & Didham 2015). In order to be most effective, chew cards, like any monitoring method, need to be sensitive to the target species while avoiding saturation of the devices at commonly encountered pest densities (Caughley 1977; Brown *et al.* 1996). However, there is no national standard of duration for chew card monitoring and published studies range from two (Ruffell, Innes & Didham 2015) to 10 nights (Kavermann, Paterson & Ross 2013; Schadewinkel *et al.* 2014). Although longer chew card exposure improves sensitivity by providing more time for pests to encounter and mark cards, durations that result in nearly all cards being marked

make it difficult to differentiate between sites with “high” and “very high” pest densities.

Sweetapple and Nugent (2011) raise the possibility that species’ detection rates may not be independent of each other, violating the assumption of a constant probability of detection. They found species may have their detection rates depressed when a card has already been interfered with by another species (also known as interspecies interference). If the depressive effect is symmetric (species A ⇋ species B) and the order of arrival is unknown, it is difficult to derive a correction factor given that species densities may vary independently. For example, existing work on species interference has found that at high rat densities, possum detections on chew cards may be depressed (Sweetapple & Nugent 2011), while unpublished work suggests that rats are deterred from chew cards by pre-existing possum chewing (Sweetapple, P, pers comm.). Rats often remove large parts of the baited areas of cards (Sweetapple & Nugent 2011) potentially obscuring any sign of previous marks left by other species on the card, as well as leaving little bait to subsequently entice other species to the card. Possums are less destructive, although heavy chewing and associated sign may deter other species from the card (Sweetapple P, pers comm.).

We sought to answer five questions related to the limitations of chew cards and the spatial patterns of possum and rodent pest abundance using data from three surveys from sites in Southland, New Zealand:

(1) What is the estimated absolute abundance of possums in the wetland?
(2) Is there evidence of interspecies interference?
(3) What is the pattern of accumulation of species detections on chew cards over time?
(4) Does interspecies interference change over time?
(5) Is there evidence of edge effects for rats and possums within the experimental sites?

3.4 Methods

Fieldwork:

The duration and interference study was undertaken at New Zealand's largest Ramsar site, Awarua-Waituna wetland complex, near Invercargill, Southland (Figure 3.1). Experimental work suggests herbivory and seed predation is significantly retarding post-fire forest regeneration within the wetland (Burge O, unpublished data). Previous surveys by the Department of Conservation using conventional methods (trapping) had found pest species (particularly, *Rattus rattus* (ship rat), *Trichosurus vulpecula* (possum), *Felis catus* (cat) and *Mustela putorius furo* (ferret)) around the edges of the wetland (Jacques 2009) and therefore the experiment was also designed to test variation in pest densities from the wetland edge.

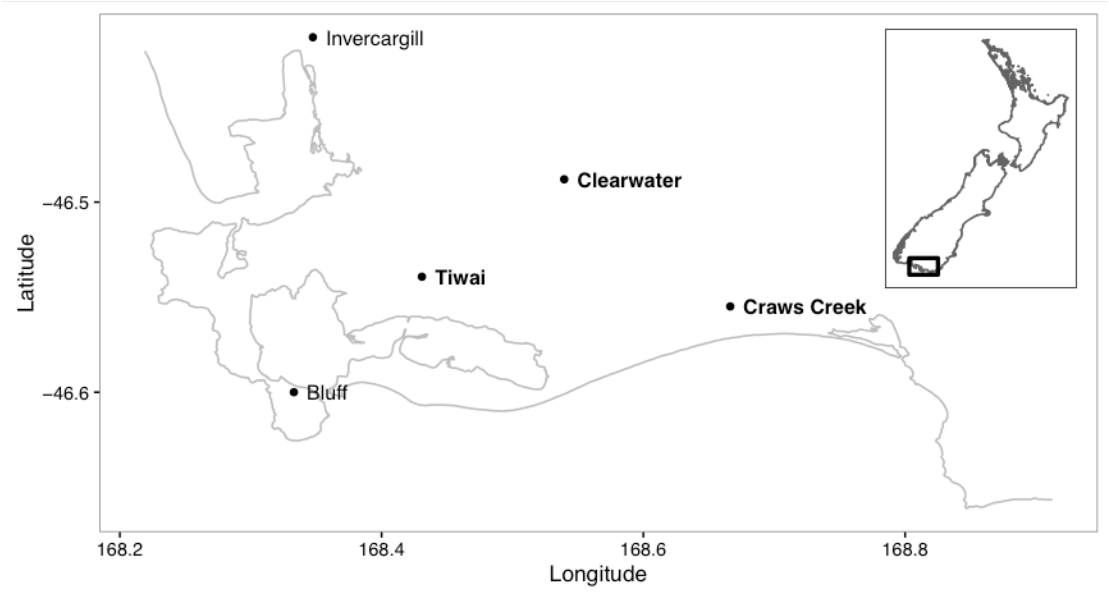


Figure 3.1: Location of the three survey sites within Southland, New Zealand and the two nearest towns, Invercargill and Bluff.

Edge effects and end-of-experiment interspecies interference

In 2012 we ran two experiments testing the effect of edge on pest densities, and end-of-experiment interference rates. In April 2012 the survey was undertaken at two sites to the west of the wetland (Tiwai) and the east (Clearwater), chosen because they contained large, relatively contiguous areas of mānuka (*Leptospermum scoparium*) considered to be suitable for forest regeneration. In November 2012 the survey was replicated on the same transect lines but an extra site abutting a forest remnant was included (Craws Creek). Transects were established at each site parallel to edges (edges were defined as the closest transect to the wetland edge (a road) in the case of Tiwai and Clearwater – bordering more wetland and farmland, respectively – and a forest remnant within the wetland at the Craws Creek site). Thirteen cards were used for each transect. Cards were spaced at 25 m intervals along each transect and transects were parallel and 100 m apart. Cards were supplied by Connovation NZ and were pre-baited with Ferafeed™, a bait designed to attract possums and rodents. In both surveys the cards were also baited with peanut butter in the middle of the card. Cards were inspected at the conclusion of the experiment in the field and where necessary inspected in the lab with a magnifying glass. Each check involved recording which species were present on the card and to what degree the card had been interfered with. If an animal left sign on a card, we scored for the area of card affected using a three-point scale: 1 (<50%), 2 (50-75%) or 3 (>75% of baited area of card chewed/eaten). In all surveys the same transects were used, located using a GPS.

Species detections over time and interactions with interspecies interference

To follow up the effect of duration of exposure and interspecies interference over time, in April 2014 we tested interspecies interference over time. We replicated the design of the first studies at the three sites with two main differences: cards were not baited with peanut butter in addition to FeraFeed™ and we chose 7 nights' duration because it was the longest period used in initial chew card methodology and interspecies interference testing (Sweetapple & Nugent 2009; Sweetapple & Nugent 2011). Cards were (non-destructively) checked daily and left in place for the duration of the experiment. This allowed us to determine (1) the rate of accumulation of detections, (2) the order of

interference where a card was marked by two different animals, and (3) whether interference probabilities changed over time. Because cards were monitored daily, we were able to compare edge effects and pest densities to the earlier 5 night durations.

Additional time required for the establishment of each site meant all three surveys sites were established and collected in a staggered fashion, one day apart. One card disappeared from the 3rd transect at the Craws Creek site in the 2014 survey and was unable to be relocated, and was therefore excluded from the analysis.

Analysis

All analyses were undertaken in the statistical computing package R (R Core Team 2015).

Estimated absolute abundance

We calculated an estimate of absolute abundance following Sweetapple and Nugent (2009), using a 5.9:1.0 relationship between seven night's duration chew card results and standard trap catch index and the 4.9:1 relationship between trap catch index and absolute possum density per hectare (Ramsey *et al.* 2005). We include this estimate so that saturation rates may be compared to sites with different pest densities in future work.

Is there evidence of interspecies-interference at the end of experiments?

Interspecies interference between rats and possums was tested analysing the likelihood of one species marking a card when a contraspecific had also marked it. We analysed rats and possums separately using generalised linear mixed effects models (GLMMs) using the R package LME4 (Bates *et al.* 2014). We used contraspecific presence as a fixed effect, and included distance from edge to account for edge effects. No significant interaction between distance from edge and contraspecific was found, and was not included in the final models. Nested random effects were included: a random intercept for transect, nested within site, nested within survey. We pooled end of experiment data for all three surveys at maximal duration (5 nights for April and November 2012 and 7 nights

for April 2014) to maximise the number of rat observations included in the model.

Quantifying the rates of detection over time

We used a GLMM to analyse the effect of experiment duration on species detections using the R package LME4 (Bates *et al.* 2014). The effect on the cumulative sum of marked cards per transect was analysed using species, day, and species by day interaction as fixed effects. Random effects were specified to account for the repeated measures and differing species responses over time: the model included a random intercept for transects nested within sites and a random slope for species within transects nested within sites. All species recorded during the study (mice, possums and rats) were included as levels within species. Predicted rates of species detections from day 1 through to 20 were calculated for each species using population-level uncertainty estimates from the model for the reasons described above. We extrapolated out to 20 days as a duration that would allow transects to saturate where species were present. R-squared values for selected GLMM models were calculated following the methods in Nakagawa and Schielzeth (2013), as implemented in R package MuMIn (Bartoń 2014).

Quantifying interference over time

Because cumulative rat detections are more at risk of interference due to their slower rates of accumulation on transects, we analysed the effects of duration and the number of accumulated detections of possums and duration X accumulated detections of possums on their rates of accumulation, using a generalised linear mixed effects model. The modelled response was the likelihood of additional individual (chew card level) detections, with duration, distance to edge and an interaction between night and the accumulated proportion of cards on the transect that had been chewed by possums the previous night. Random effects included an intercept for transects nested within the sites to reflect the spatial structure of the experiment, and an intercept term for each card, to account for repeated measures.

Quantifying edge effects

Edge effects were analysed using generalised linear mixed effect models (GLMM) with proportion of cards chewed by the target species as the response weighted by total cards, per transect, with a fixed effect of distance from edge. Date of survey (April 2012, November 2012, and April 2014) was included as a fixed effect. Data were sufficient to include an interaction term between distance and survey date for possums only. This analysis took into account data from all three surveys, for possums and rats, and 2014 data were truncated at 5 nights for consistency.

3.5 Results

At Awarua, levels of possums, rats and mice were relatively consistent across the wetland across all surveys (Figure 3.2). The 2014 data have been truncated at 5 nights for comparison purposes to the earlier surveys.

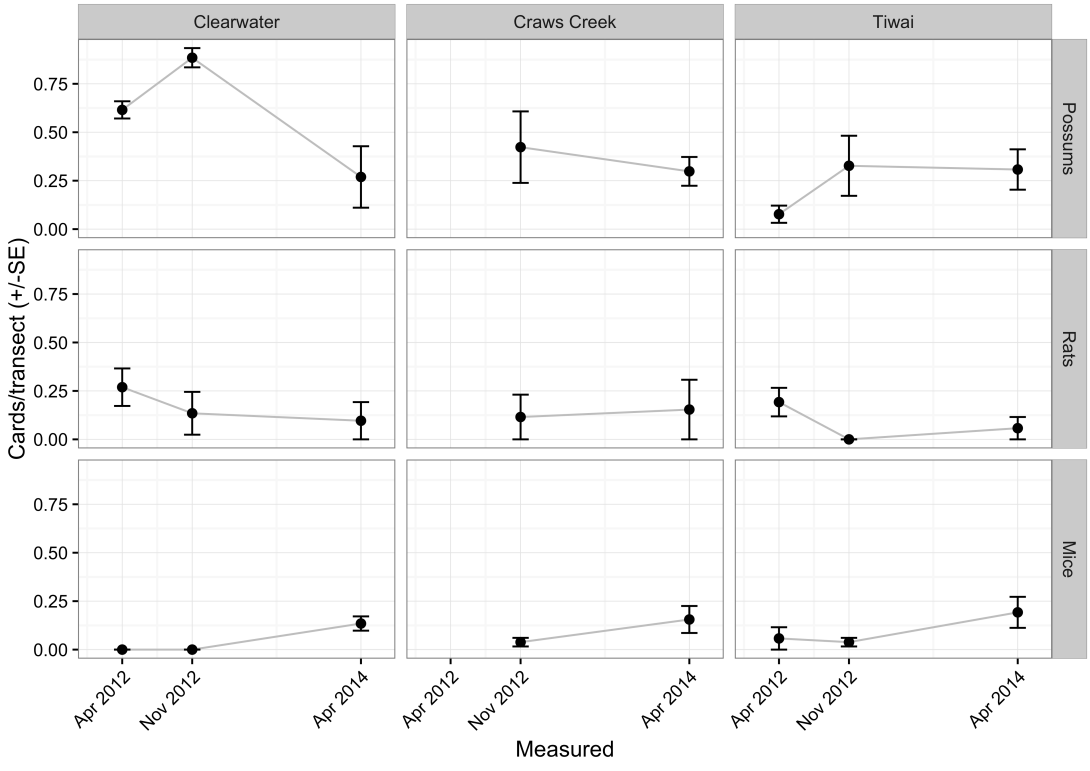


Figure 3.2: Average relative abundance (proportion of cards marked) across transects within sites of rats, possums and mice within Awarua wetland.

Estimated absolute possum abundance varied between 0.27 possums/ha (Tiwai, April 2012) and 3.1 possums/ha (Clearwater, April 2012). The highest possum

site (Clearwater) dropped to lower levels in the 2014 survey, consistent with a sustained trapping effort along the wetland edge. Possum estimates in 2014 ranged from 0.5 possums/ha (Tiwai, most distant from forest edge), to 2.13 possums/ha (two transects closest to the edge at Clearwater and one at Tiwai closest to the edge).

Is there evidence of interspecies-interference at the end of experiments?

Across all time periods, we found evidence of significant interspecies-interference between possums and rats (Figure 3.3). After accounting for edge effects, possum sign on cards significantly reduced the likelihood of rat sign ($z = -3.122$, $p < 0.002$). Rat sign similarly reduced the likelihood of possum sign ($z = -3.703$, $p < 0.001$). Overall, this interference effect reduced the predicted likelihood of a rat marking a card from 9% to 3% and the likelihood of a possum marking a card from 44% to 18% (averaged across all transects).

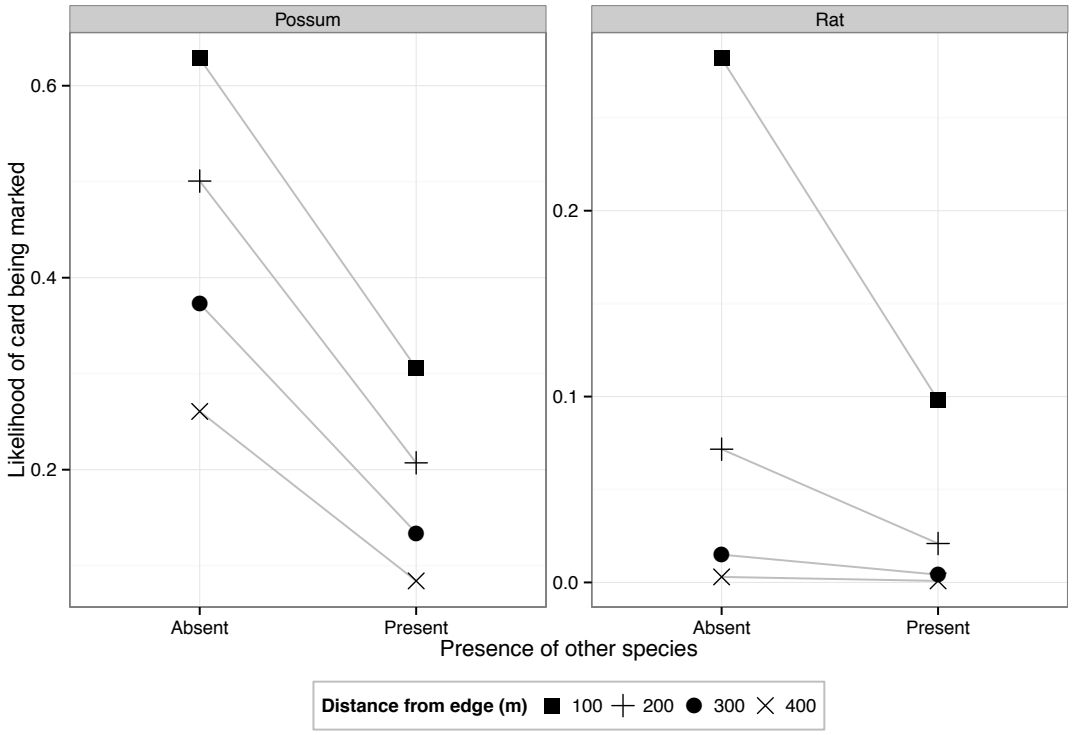


Figure 3.3: Likelihood of a card being marked by one species (rats or possums) conditional on the presence of a contraspecific and distance from edge. The presence of a contraspecific and distance from edge both significantly reduced the likelihood of a card being marked (see text). Note that unless all cards on a transect are marked by one species, the transect-level interference effect will be smaller than the card-level effect shown here.

How much the interference effect affects the reliability of the survey as a whole will depend on how many free cards per transect remain – a function of both species' density and experimental duration – and we address this in the second research question.

Limited co-occurrence data from the 2014 survey meant we had little information on order-of-occurrence. Possums were detected on 61 cards, rats were detected on 13 cards and of these, six cards had signs of both species. Rats were found first on one card; possums were first on two cards; and the remaining three occurred on the same night, making order indistinguishable. Furthermore, the cards on which order of occurrence was distinguishable all had been scored as being heavily chewed the previous night, showing that heavy chewing by one species does not completely prevent subsequent detection of another species.

Quantifying rates of detection over time (possums, rats)

As a proportion of total cards with sign, possum detections accrued faster than rats or mice for the first half of the experiment (Figure 3.4(a)). No rats were detected until after the third night's exposure. In the 2014 experiment, of all possum detections over 7 nights (n = 62), 72% had occurred by the 5-night mark, and for rats (n = 19) this figure was 89%.

We modelled the change in total cards detecting a species per transect, per night as a response to fitted effects of species and duration (number of nights exposure). Model fit was worse when we excluded either species or night (delta AICc 6.15 and 260.87, respectively) from the model. There were significantly fewer rats and mice than possums (rats: $z = -3.633$, $p < 0.001$; mice: $z = -3.390$, $p < 0.001$). There was a significant interaction between species and night (rat c.f. possum, $z = 2.265$, $p = 0.02$), meaning the rate at which rats and possums accrued by night was species-specific (Figure 3.4(b)). Conditional r-squared (total explained by the model, taking into account fixed and random effects) was 78%. Marginal r-squared (the amount of variation explained by the fixed effects alone) was 38%.

We fitted the same model but included only transects on which species were present (at least one card, by species) to demonstrate the different rates in accumulation of species sign on transects (Figure 3.4(b)), and the speed at which transects would saturate given a longer duration (Figure 3.4(c)). R-squared values for this model were lower than that which included presence/absence (conditional: 39%, marginal: 25%), due to excluding different transects for zero detections by species.

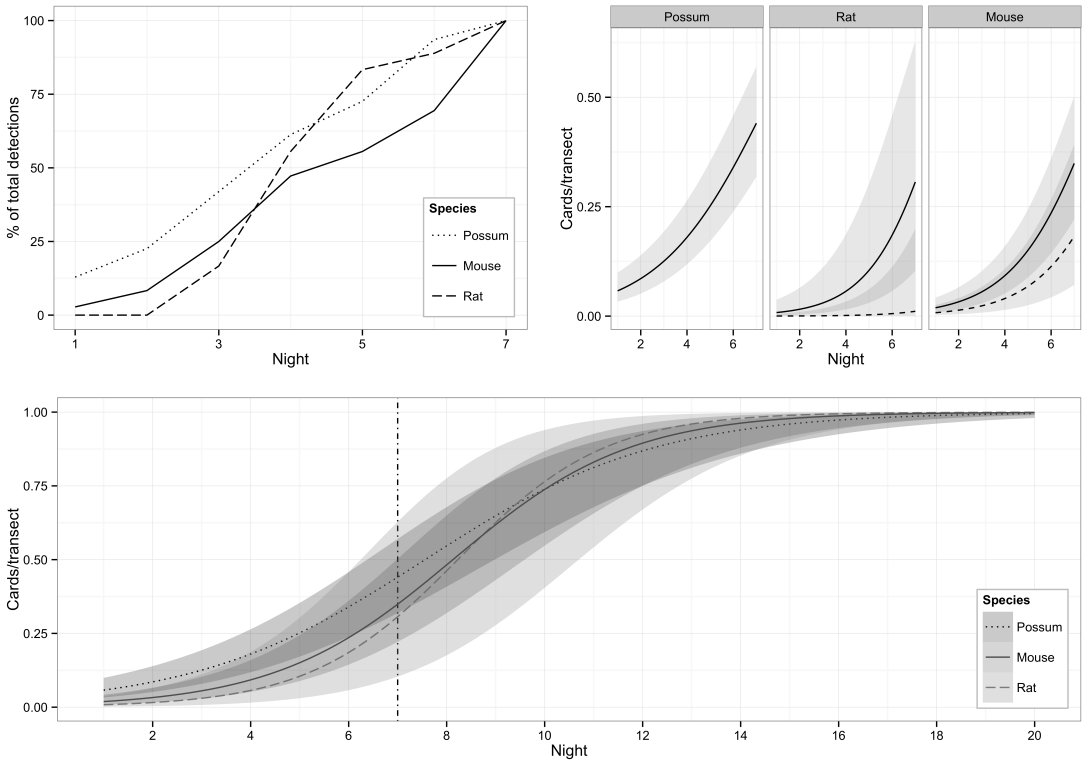


Figure 3.4: (a) Relative cumulative species detections as a percent of total cards marked by duration (2014 data) and (b) Fitted detection rates by species and night (2014 data) as a proportion of cards per transect, for: transects on which species were present (solid line); and all transects (dashed line). We include only one line for possums as they were found on all transects. (c) Presence-only data are used to model transect saturation by predicting out to twenty night's duration. Dashed line indicates extent of raw data.

Quantifying interference over time (possums and rats)

Because possums were found on transects both with and without rats, we were able to model the effect of interference by rats as it interacted with survey duration, on the likelihood of an additional possum detection per transect. We

used this model (model coefficients in Table 3.1) to predict the likelihood of possum detections across a range of rat densities (Figure 3.5).

Table 3.1: Generalised linear mixed model summary of the effect of duration, transect and accumulated interspecies detections on the likelihood of additional possum detections.

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-1.96	0.39	-5.09	0.000	***
Duration	0.08	0.07	1.14	0.256	
Distance to edge	-0.43	0.14	-3.09	0.002	**
Duration:Accumulated rat detections	-0.89	0.37	-2.40	0.016	*

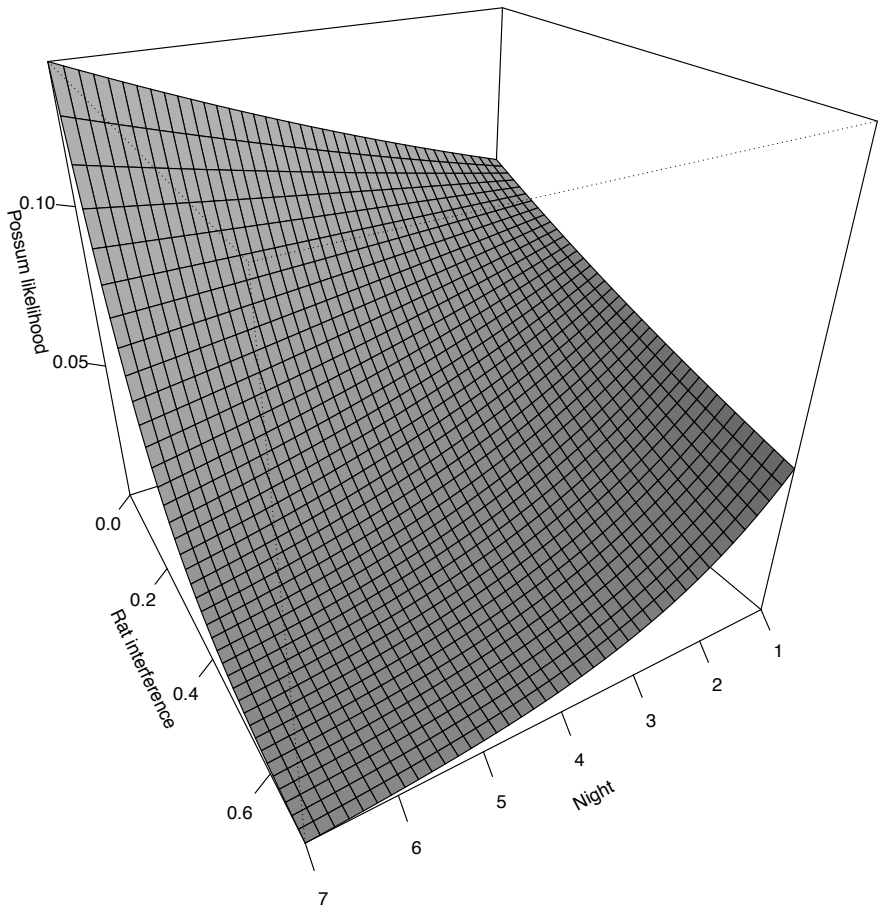


Figure 3.5: Fitted effects of exposure time and rat interference on the probability of possums marking a card. At low rat densities, possum detections increase with longer exposure, consistent

with the modeled cumulative possum detection rates not beginning to saturate until around night 11 (Figure 3.4(c)). At high rat densities and long exposure times, there are few rat-free cards available for possums, so increasing interference (Figure 3.3) causes a decrease over time in the chance of additional possum detections.

Quantifying edge effects

Edge effects significantly affected rat detections, with detections decreasing as distance from edge increased (Figure 3.6, z = -3.545, p < 0.001). The overall model performance was worse when the distance term was removed (when assessed using AICc [delta AICc = 6.21]). Edge effects for rats were so pronounced in the April 2014 survey that only one card was marked by rats outside of the first ("edge") transect, across all three sites. Edge effects were significant for possums only in the 2014 survey (z = -2.433, p = 0.015). Model fit was only slightly poorer with the distance term removed (delta AICc = 0.39).

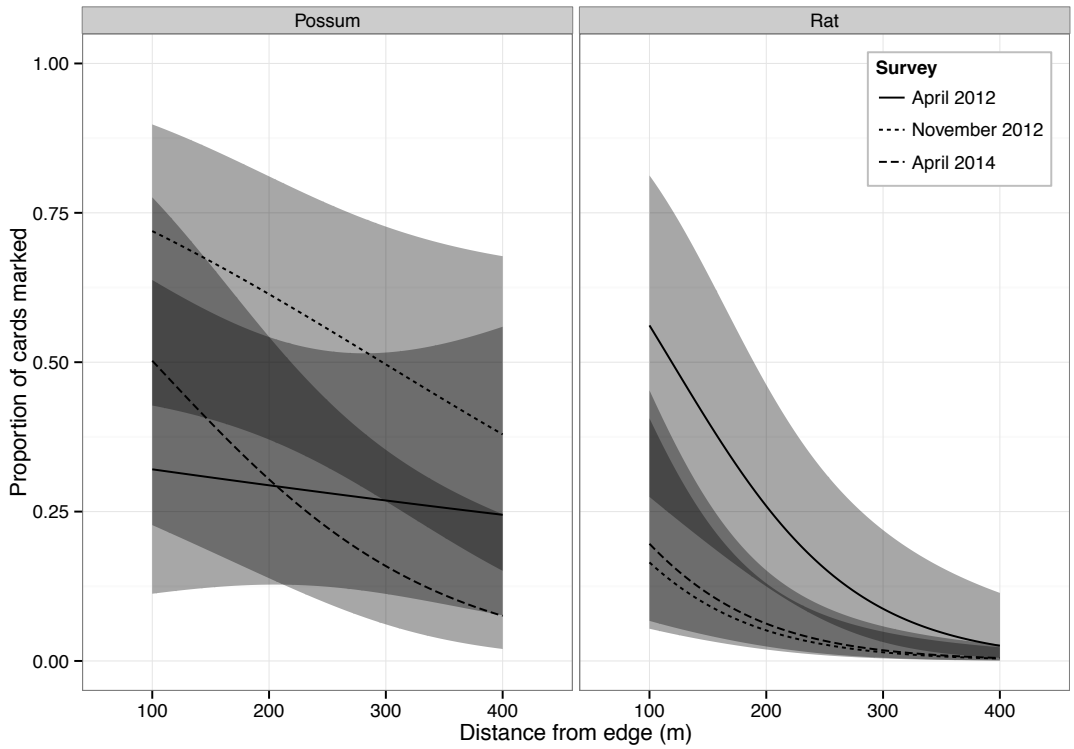


Figure 3.6: Predicted edge effects and 95% confidence from generalised linear mixed effects models, expressed as the proportion of cards detecting a species for a given distance from edge.

Non-bite species detections

Mice bite marks were detected on 39 cards in the survey, of which 3 also had evidence of mice faeces. A further 7 cards had no sign of chewing by mice, but

had faeces. Taking into account faeces-positive as well as chew-positive cards increased mouse detections by 18%.

3.6 Discussion

Is there evidence of interspecies-interference at the end of experiments?

Chew cards are rapid to deploy in the field, and easily interpretable (Sweetapple & Nugent 2011). They have been found to be more, or at least as, sensitive to target species than wax tags and tracking tunnels. However, their unbiased accuracy has been questioned with regard to varying degrees of interspecies interference which would violate the assumption of constant proportionality, meaning comparison of results across time and space may not be robust (Pendleton 1995; Ruscoe, Goldsmith & Choquenot 2001; Norvell, Howe & Parrish 2003).

We demonstrated significantly reduced co-occurrence on cards between rats and possums within Awarua wetlands (Figure 3.2). This is consistent with previous work on chew cards (Sweetapple & Nugent 2009). As Awarua 2014 is the only study measuring order of arrival or priority effects and so few cards were bitten by two species in our study, we were unable to quantify the deterrent effect on a per chew card level. The relevance of order of detections with regard to interspecies interference may be best addressed in the future with laboratory experiments using captive animals (cafeteria experiments), or use in the field where a secondary method of species monitoring is used to derive a correction factor.

We speculate that the physical mechanism of interference may not solely be amount of bait remaining, given all the cards with sign of both rats and possums had been chewed "heavily" the night before if they had been chewed at all. This would suggest that introducing species-specific baits for cards rather than increasing the area of card that is baited will be more effective in reducing the interference effect.

Quantifying the rates of detection over time

We found significant differences between species in the rates at which their detections accrued on transects, and in their final relative abundances. We found a slower rate of accumulation by rats in our experiment, which took three nights to be first detected. Although surprising, we consider this lag not to be an artefact of experimental factors, given sites were set up sequentially over three days and standard baited chew cards were used. Rats, and particularly Norway rats (*Rattus norvegicus*), are known to be neophobic, with the strongest neophobic reaction to new objects in a familiar environment (Innes 2001). Ship rats (*R. rattus*) are considered to be less neophobic (Moors, Atkinson & Sherley 1992). There is little published information on neophobia in the Pacific rat (or kiore, *R. exulans*) (Clapperton 2006), but neophobia has been found to affect detections for similar durations as this study (zero captures until after two days of trap exposure: Adams *et al.* (2011)). Both ship rats and Norway rats have been recorded within the wider wetland area (Jacques 2009). Other surveys with detections after the two nights (for example, Ruffell, Innes and Didham (2015)) may either have only sampled less neophobic species, or populations (depending on proximity to edge and size of remnants in which surveys are located), and may have underestimated density if a proportion of the population are neophobic.

The estimated corrected possum abundances in April 2014 (1.9 – 3.0) were higher than those previously reported for grassland and shrubland (0.4 – 1.7 possums per hectare) but less than those reported for podocarp-broadleaf forest (3.3 – 16 possums per hectare) (Rouco *et al.* 2013). We therefore consider these results are conservative except with respect to speed of saturation, the importance of which we discuss below.

Quantifying interference over time

Increases in rat detections significantly decreased the likelihood of additional possum detections on transects, and this effect varied with duration. While we were only able to model the effect of rats on possums, we consider this a conservative scenario, given that rat detections suffer from the initial lag

discussed above and for the first four nights rat sign accrue more slowly than possum signs.

Quantifying edge effects

We found significant edge effects for rats and possums within the wetland. This is consistent with prior pest surveys. The edges at which we measured were closer to drains and the road (at two sites) and a drier area of remnant forest which also provides a food source (Craws Creek). The significant edge effects we detected (Figure 3.5) affected rats more than possums, which made it possible to assess what the possum detection rate might be like in the absence of rats. Rats were near-absent from non-edge transects (Figure 3.5). Possums decreased further from edges but not significantly so.

Non-bite species detections

Chew cards have been found to be up to 50 times more sensitive to mice than unbaited waxtags, and are considered to be equally or more sensitive than tracking tunnels (Sweetapple & Nugent 2011). Furthermore, we found faecal evidence of mice on cards that otherwise showed no sign of being chewed by mice. Taking account of these cards in our study significantly increased the number of mouse detections we made by 18%. Therefore, we suggest that sensitivity of chew cards to mice will be greatly increased during their deployment in the field if mouse faeces as well as chew marks on cards are recorded in the field.

Recommendations and conclusions

Contra-indications to chew card usage

Chew cards violate the principle of constant proportionality due to interspecies interference effects. Where either possums or rats are likely to saturate transects before a reliable estimate of the other can be obtained, other survey methods should be considered (including shorter survey duration). If rat detections do not saturate transects, the most conservative option will be to derive possum abundance from only those cards which have not detected other species (i.e. total cards interfered with by possums only/total cards interfered by

either possums or no other species). Conversely, where chew card transects are used solely as a presence/absence measure (e.g. as a pest incursion indicator on predator-free islands) concerns around interference skewing the relative abundance measure are less of an issue.

Recommended experimental duration

Current chew card survey duration rates currently vary due to saturation risk, cost and pragmatic considerations. Long-term or multi-site monitoring requires a relative abundance index be comparable between surveys, and there would be benefits in a nationally consistent approach. In the interim, although the risks of interspecies interference and saturated transects may point toward a shorter duration, we recommend avoiding durations of less than three days to avoid false-negative transect absences of rats, particularly where Norwegian rats or Pacific rats are likely to be present in the absence of ship rats. However we recognise that in sites with higher pest densities the risks of saturation will be high – Ruffell, Innes and Didham (2015) note that several transects approached saturation after a two night experimental duration. This makes a 'one-size fits all' duration difficult to settle upon. We would therefore suggest a duration of five nights to adequately balance the risks of false-absence findings and saturation in low-moderate assessed densities. High pest density sites may require a shorter duration, but current data is lacking to quantify the risk of interspecies interference as it interacts with duration at these densities. While this may lead occasionally to experiments with different durations, the non-linear rate of species detections over time and interactions with contra-specifics cautions against 'adjusting' species detection rates in an attempt to reconcile them.

How much of a concern is saturation?

Does the risk of transect saturation preclude a nationally consistent duration? It may be that consistency (which allows comparison between surveys) is considered to trump concerns around saturated transects (which allows differentiation between sites of high density and very high pest density). We suggest that a nationally consistent duration which reduces the risk of underestimating neophobic populations is of most importance. The need to distinguish between sites of 'high' and 'very high' pest abundance where

transects will saturate is rare and could be provided for as a recognised exception in the standard.

The special case of sites where pest densities are expected to vary significantly

Situations where pest densities at sites are likely to be variable include pre- and post- pest control, where pest densities are expected to be high initially, but low afterwards. In such cases, a shorter duration of chew card deployment may be required to reduce the risk of saturation at the pre-control measure. However post-control, we suggest that the same monitoring period is undertaken (for comparison with the pre-treatment survey) but cards left in the field for a longer period (e.g. a check at 3 nights, and at 5 nights) for better sensitivity to species' presence on transects that might go undetected at short durations and with lower pest densities.

Mice detections

We recommend recording mouse and other pest faeces in addition to chew marks on cards to maximise sensitivity. While the ability of chew cards to detect multiple species leads to some of the cautions above, these can be addressed by choosing an appropriate experimental duration, and accounting for the effects of rats and possums on the others' detection rate in modelling.

Overall, chew cards are an effective and cheap monitoring tool, with the caution that where rat or possum densities are high, relative contraspecific abundance is likely to be underestimated. We consider that a nationally consistent approach to chew cards is desirable. In the absence of such a standard we recommend adjusting duration to expected pest densities and monitoring goals, but using a duration of at least 3 nights (and preferentially 5 nights) to take account of neophobic species and populations.

Chapter Four: The folly of charismatic methods: bird perches

4.1 Introduction

Ecological restoration has been defined by the Society for Ecological Restoration as being "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (2004). However, the default position in restoration ecology is to "do nothing" and let natural processes lead to succession to a previous or desired state (Brown & Lugo 1990; Finegan & Delgado 2000; Suding, Gross & Houseman 2004; Vieira & Scariot 2006; Hobbs & Cramer 2008), but this approach may either take longer than considered desirable, or proceed on a trajectory not considered desirable (Parrotta 1992; Carnevale & Montagnini 2002; Sullivan, Williams & Timmins 2007; Rodrigues *et al.* 2009). Restoration should be undertaken only after constraints on natural regeneration are known (Hobbs & Norton 1996).

Forest regeneration is a multi-stage process with a number of potential ecological filters or constraints on success (Figure 4.1). Seeds must first arrive at a site, which requires a more or less proximate seed source and a vector (wind, water, or animals). Most New Zealand trees (circa 59%) rely on animal dispersal (Kelly *et al.* 2010), which is a similar percentage to temperate forests more generally (Howe & Smallwood 1982).

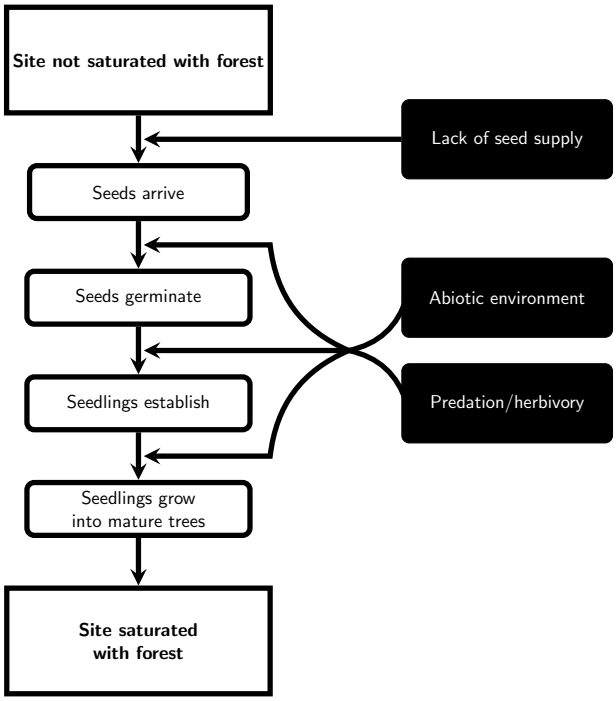


Figure 4.1: The regeneration process (white boxes) and relevant constraints (black boxes). Constraints may be absolute (filtering effects so strong no individuals reach the next stage), or relative (the proportion of individuals making it through to the n next stage is reduced proportionate to the strength of the constraint). Figure reproduced from Chapter 1.

Once at a disturbed site, seeds must germinate, grow, and survive to become a seedling and thereafter grow to maturity (Grubb 1977). There are multiple ecological filters on forest regeneration and the relative importance of each varies between species and sites (Holl 1999). This process is sequential: species can only pass through a filter such as seedling herbivory after they have passed through an arrival filter, and then an abiotic filter to germinate (Fattorini & Halle 2004).

A lack of seed arrival is a common barrier to forest regeneration (Aide & Cavelier 1994; Holl 1999; Wijdeven & Kuzee 2000; Cubina & Aide 2001; Howe & Miriti 2004; Hooper, Legendre & Condit 2005; Kelm, Wiesner & Helversen 2008). The process of seeds arriving at an uncolonised site may be disrupted by fragmentation (creating a lack of seed sources) (Wunderle 1997; Duncan & Chapman 1999; Holl 1999; Wijdeven & Kuzee 2000) and reductions in frugivorous disperser populations (a lack of vectors to disperse seeds from seed

sources to the site) (Duncan & Chapman 1999; Holl 1999; Moran, Catterall & Kanowski 2009; Markl *et al.* 2012). Even where seed sources and dispersers are present in the landscape, dispersing animals may avoid open, disturbed areas due to a lack of enticement (e.g. food, perching sites) or potential increased risk (e.g. predators) (Aide & Cavelier 1994; Nepstad *et al.* 1996; Wunderle 1997). Seed dispersers' proximity both in space and time is relevant: attracting frugivorous birds is not sufficient to increase forest seed deposition if they have not recently fed at seed sources (Graham & Page 2011).

Environmental constraints can also limit both the seed germination and seedling establishment phase. In open areas these include dessication and hydrological conditions (Roy, Ruel & Plamondon 2000), edaphic variables and nutrient status (Holl *et al.* 2000), photoinhibition (Ball 1994; Howell, Kelly & Turnbull 2002) and larger temperature ranges (Uhl, Buschbacher & Serrao 1988; Steven 1991b; Steven 1991a; Cramer, Hobbs & Standish 2008). In a review of sowing experiments, Turnbull, Crawley and Rees (2000) found that conditions for seedling establishment had a stronger effect than for germination, meaning at some sites, germinated seeds will be a poor indicator of a site's suitability for seedling growth and survival (Graham & Page 2011).

Seed predation has been found to significantly reduce seeds available to germinate (Janzen 1971; Steven 1991a; Myster 2004; de Souza Gomes Guarino & Scariot 2014), although there is mixed evidence in New Zealand forest species (Allen, Lee & Rance 1994; Moles & Drake 1999; Williams *et al.* 2000). Seedling herbivory can have lethal or sub-lethal effects on tree seedlings and influences tree seedling composition in existing forests and disturbed sites (Cadenasso & Pickett 2000).

Forest restoration methods

Forest restoration methods include planting seedlings and sowing seeds. Seedling planting is the most commonly used method for the recovery of degraded areas (de Souza Gomes Guarino & Scariot 2014), and used almost twice as often as direct seeding (56% and 31% respectively, Ruiz-Jaen & Mitchell Aide

(2005)). Bird perches have been described as "a useful and inexpensive management technique for manipulating natural seed dispersal" (Shiels & Walker 2003 p 8). Perches have been studied in the tropics (Carlo & Yang; Wunderle Jr 1997; Holl 1998; Shiels & Walker 2003; Zanini & Ganade 2005), and less recently in temperate ecosystems (McDonnell & Stiles 1983; McClanahan & Wolfe 1993). However, unlike seed and seedling addition, bird perches can only indirectly mediate seed dispersal by *potentially* increasing bird activity (see Figure 4.2).

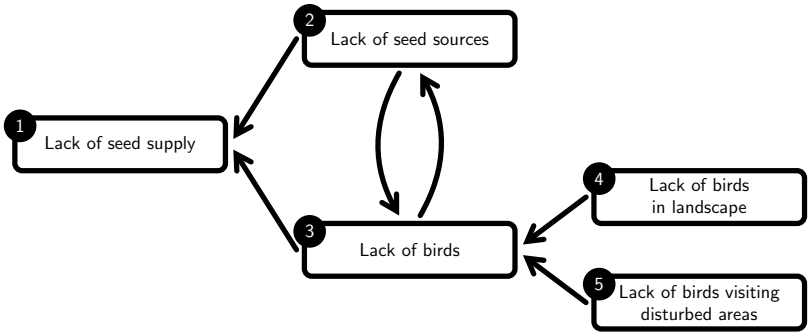


Figure 4.2: The seed supply filter (1). For seed to arrive at an uncolonised site, it requires there be both a seed source in the landscape (2) and a vector (3), in this case, birds to disperse it. A lack of birds will lead to a lack of seeds entering the site even if they are present in the landscape; birds passing through the landscape cannot disperse non-existent seeds. Note that perches can at best affect (5) - whether birds that are already in the landscape are more likely to visit disturbed areas. Any positive contribution to increased seedling establishment (and thereafter survival) is wholly reliant on supervening factors: whether there is a source population of birds to draw on (4); whether birds deposit seeds; whether birds deposit forest seed; and whether biotic and abiotic conditions are suitable for germination and establishment.

Bird perches have been demonstrated to increase seed deposition in open areas (McDonnell & Stiles 1983; McDonnell 1986; McClanahan & Wolfe 1993). The aim is to have birds visit having fed from elsewhere, and excrete seeds while resting on or flying to or from perches (Wenny 2000; Cavallero, Raffaele & Aizen 2013). The success of perches as a restoration tool can only be assessed where experiments measure seedling establishment under perches compared to controls, instead of only measuring bird visits, or total seed deposition. However, there are few data verifying the supposed cost efficiency or even effectiveness of perches as a restoration tool in temperate areas (see Graham and Page (2012) for an example in the tropics). Here, I test perches in Awarua wetland, a 20,000 ha Ramsar-recognised wetland in the South Island of New

Zealand. The wetland is considered to have once supported forest on the drier parts of the site, but following anthropogenic burning only small isolated forest fragments now remain. I investigate whether bird perches could be used to speed regeneration of native forest by ameliorating possible dispersal limitation at the site. Active restoration is considered desirable at this site because speeding regeneration by less flammable later-successional native trees would reduce the risk of fires that stall successions (Perry *et al.* 2015). My study is rare in that I also compare the efficacy of bird perches with direct seeding, seedling addition and pest control that I had experimentally tested at the same site.

4.2 Methods

My perches deviated from common practice in that rather than being placed in pasture, perches were placed in mānuka (*Leptospermum scoparium*) shrubland, a mid-successional species and a nurse plant for forest species that covers approximately half of the wetland (Anon. 2010). Abiotic thresholds were considered to be less of an impediment than in a pasture environment as there was evidence of a low-density natural regeneration within the mānuka (refer Chapter 2, vegetation survey). New Zealand's largest extant native frugivorous bird (kereru, *Hemiphaga novaeseelandiae*) was the target species for perches. Kereru are known to fly long distances between patches (Powlesland, Moran & Wotton 2011; Wotton & Kelly 2012). Unlike perches designed to entice birds from abutting forest remnants, perches were designed to offer a rest point during long flights over the wetland. Wide-ranging dispersal species are considered to be more important for transporting forest seeds into degraded areas than species already present in the areas (Guevara & Laborde 1993).

I selected two sites predominantly covered by mānuka that were considered to be (a) suitable for regeneration and (b) seed dispersal limited (based on the results in Chapter 2). At each site four perches were erected in April 2012 at varying distances from the vegetation edge. Perches were constructed in situ, using 6.5 m lengths of treated timber for the upright posts, and a 40 x 3 x 4 cm cross hatching at the top for the perch (see Figure 4.3). Perches were sunk 1 m into the peat soils and secured with metal fencing stakes and guy ropes. Perches

were not baited. Two seed traps of 50 cm diameter were erected under each perch. The top of the trap was 90 cm from the ground and at its nearest point, 50 cm from the perch. A pair of control seed traps was set up in the same configuration in a random direction 20 m from each perch. Traps were not designed to exclude pest species as I sought to replicate seed arrival under current environmental conditions. Perches were emptied approximately every two months for the duration of the experiment (two years). Seed trap samples were dried and sorted, and seeds were counted and identified. Any animal faeces were crushed and inspected for seeds that were then also identified and noted.

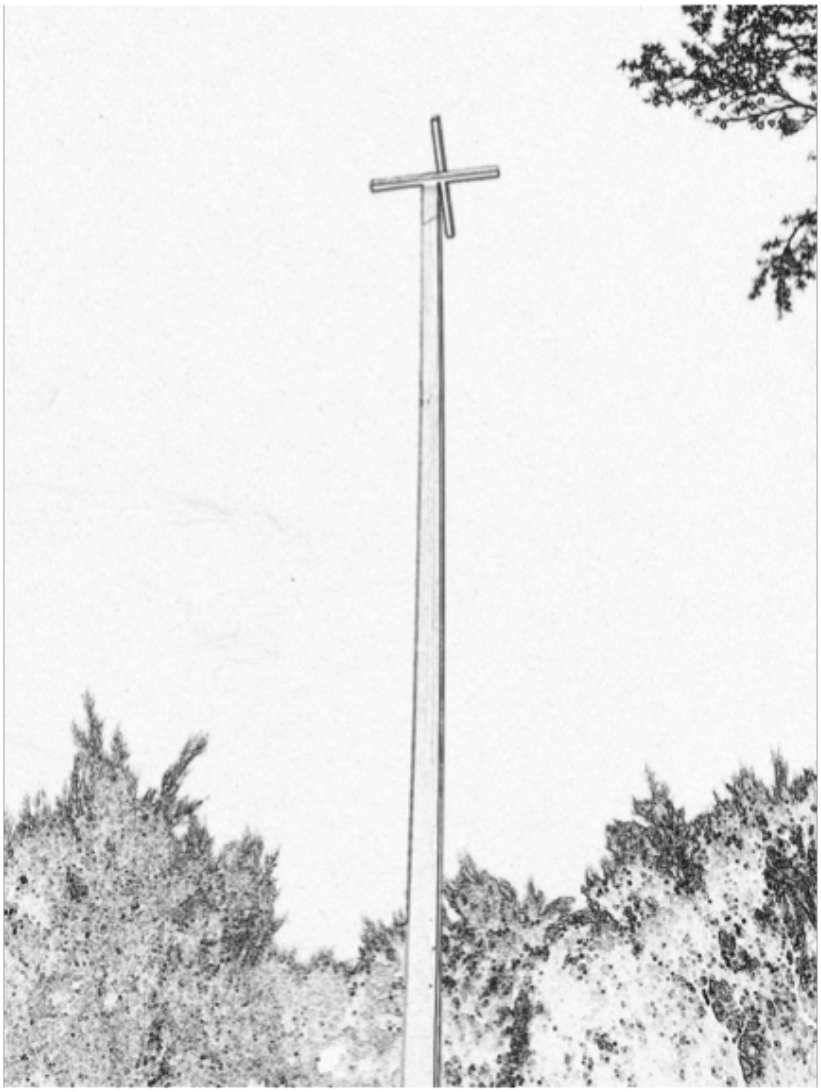


Figure 4.3: A constructed perch (6 m high) at the Clearwater site, in a natural canopy gap.

Trail cameras (Faunatech, 8MP Scouting Camera, DTC-560K) were set up on perches considered to be the most likely to attract birds from 9 – 16 November

2012 (2 cameras, 14 camera-nights). Trail cameras were set to capture 15-30 seconds of video when triggered (a combined trigger of heat and motion). Video footage was collected every two days and examined for perch visitors.

Seed and seedling addition experiments were also conducted at a number of sites within the wetland, including those where the perches were located. They are included for purposes of comparing their efficacy to perches only, and are discussed briefly (see Chapters 2 and 5 for full discussion). The seed addition involved adding 14,000 seeds to various treatments in the wetland, half of which were caged to protect them from seed predation and seedling herbivory. I created unsown caged and uncaged controls at each plot. Each replicate (e.g., sown, caged) was demarcated by 4 cm wide strips of lexan polycarbonate (1 mm thick) with the ends stapled together to construct 10 cm diameter upright tubes. Seeds were collected from local seed sources within the wider wetland area, and the only cost for this was labour. The seedling addition experiment included sites within the areas used for the seed addition and perch experiments.

4.3 Results

Relative costings

One hundred and sixty-eight seedlings were planted in mānuka at a cost of $371.30 for seedling purchase ($2.05 - $2.43 per seedling depending on the age at purchase). Labour costs per group of 4 – 5 seedlings have been estimated at 8 – 10 minutes (uncaged) and 30 minutes (caged), which at a rate of NZ$20.00 per hour averages $0.67 per uncaged seedling and $2.00 per caged seedling. These costs exclude travel time to sites and equipment haulage, which vary substantially depending on access considerations. Access will be slightly more expensive for perches due to the amount of equipment required (more trips per site) but otherwise applies equally to all methods.

Did perches increase forest seed arrival?

No seeds of forest species (or woody species) aside from *L. scoparium* were found within the seed traps (both under and away from perches). Total seed trap area measured was 6.28 m^2 (including control traps) and measurement duration

was 24 months. No birds were observed by the trail cameras, despite some 2700 'incidents' (mānuka branch movement), owing to a differential heat signature between the sky and the surrounding mānuka. *Trichosurus vulpecula* (brushtail possum) faeces were found in all pairs of seed traps under perches. Only one of the 16 control seed traps contained faeces, indicating increased possum activity occurred around perches. No seeds of woody forest species were found in any of the possum faeces.

Did seed addition increase forest establishment?

No seeds germinated in the caged or uncaged controls for my sowing experiment over 2.6 years (96 unsown replicates each of 10 cm diameter, 0.754 m^2 total), meaning sites were seed limited in terms of forest regeneration (see Figure 4.4). Overall, 15.7 ± 0.7% (all values are raw values ± standard error) of caged seeds germinated and survived at 30 months post-sowing (see Figure 4.4(a) for modelled 95% CI). The level of regeneration was also slowed by seed predation and herbivory: uncaged survival was less than half that of caged seedlings, at 7.3 ± 0.8%. Seedling biomass was significantly greater when seeds were caged: the average total height of a caged seedling replicate was 7.84 ± 0.43 cm, while the average total height of an uncaged seedling was 3.24 ± 0.39 cm (see Figure 4.4(b) for modelled 95% CI).

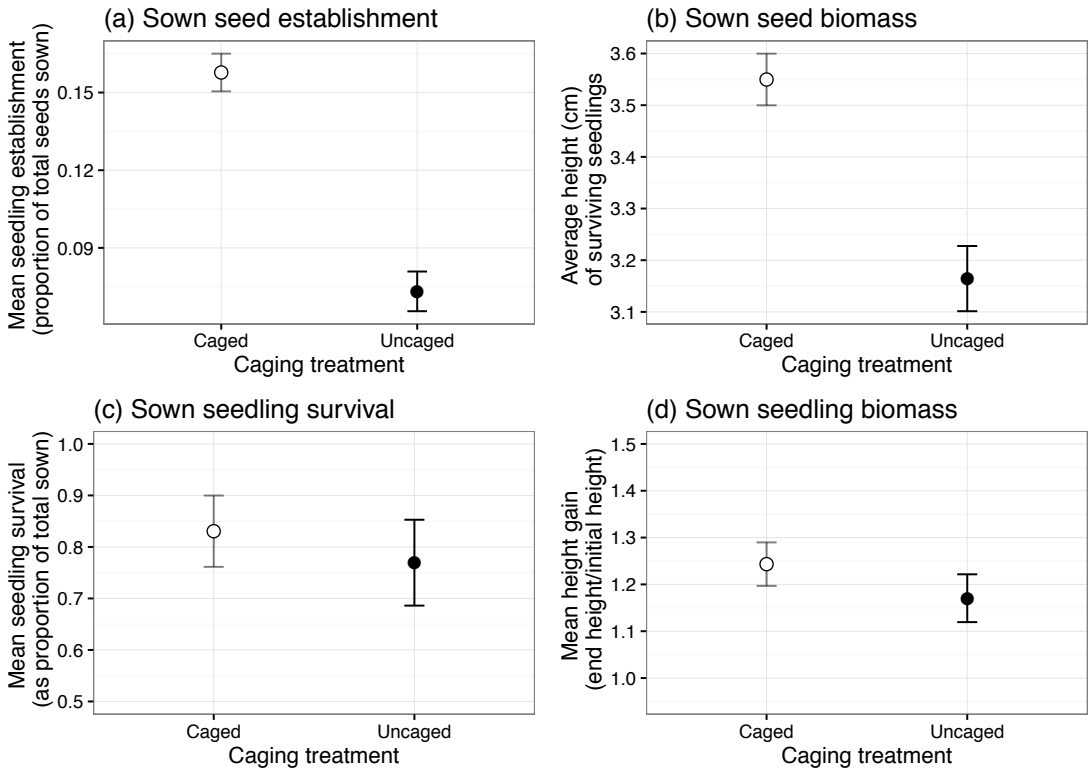


Figure 4.4: Forest establishment is increased by seed addition (a) and (b) and seedling addition (c) and (d). Modelled responses from generalised linear mixed effects models ± 95% CI are shown. Differences are significant for sown seed survival and biomass, and not significant for sown seedling biomass. Seed germination and survival (seedlings surviving as a proportion of those sown), and biomass (mean height per seedling in cm) is shown at 30 months post-sowing. Seedlings were checked for survival and biomass accumulation (gain in height from date of sowing) 12 months post-sowing. Seedlings are more expensive in terms of purchase and labour costs, but are less affected by herbivory.

Did seedling addition increase forest establishment?

The survival rate of seedlings was 83.1 ± 6.9% (all values are raw values ± standard error) for caged seedlings in mānuka areas, and 76.9 ± 8.3% uncaged seedlings (see Figure 4.4(c) for modelled 95% CI). Caged surviving seedlings increased their biomass (as measured by seedling height) by 24 ± 4.6% in the first year after planting, and by 17 ± 5.1% for uncaged seedlings.

Did perches increase forest establishment?

Forest establishment was seed limited, but without any forest seeds arriving, forest species' establishment could not increase under perches. Planted seeds of

forest species germinated and survived; and planted seedlings grew and survived when protected from herbivory (Figure 4.4(a-b)) indicating the abiotic conditions of the perch sites were suitable for forest establishment.

Are perches a cost-effective restoration tool?

Each perch cost NZ$59.75 for materials and NZ$125.00 in labour. Perches took around 5 hours to set up in the field, including locating suitable areas within sites, transporting gear within the site to perch location, constructing and erecting the perch, and erecting the perch and control seed traps. Perches were set up by one person; doubling the number of workers would decrease the amount of time required per perch but increase labour costs. Per seedling, perches were the least cost effective compared to other methods (Table 4.1). I note that although the costs per seedling between sown seeds and sown seedlings are substantial, there is a distinct size difference: sown seeds that survived to 2.6 years were on average 3.55 cm tall (caged) and 3.16 cm tall (uncaged). Conversely, seedlings grown for two years in the glasshouse were on average 38.5 cm tall. This difference is not surprising but should be kept in mind when considering the relative price difference.

Table 4.1: Comparison of costs for methods to address seed limitation. Note the lower survival rate of seeds offsets their lower cost, and the relative expense of perches for an uncertain outcome. Labour costs exclude travel to and from sites, which will be uniform for all methods. Predator and herbivore protection is estimated for small areas only (physical protection of seeds/seedlings); larger areas would require other control, such as trapping or poison. Total cost per 100 seedlings includes the materials and labour cost of protecting seedlings, and a nominal hour of labour for seed addition. Note that seed addition established seedlings are much smaller than the seedlings added, even after 2.6 years.

	Cost of materials (NZ$)	**Labour costs ($NZ)**	**Costs of seed predator and herbivore protection ($NZ)**	**Surviving # seedlings per $NZ100**
Perches	60.00/perch	125.00/perch	c. 110.00 Difficult to protect entire area around perch; I estimate 2 hours of labour ($50.00) plus $60.00 in materials (equivalent of two seedling cages).	Unknown, probably 0 (caged) 0 (uncaged)
Seed addition	0.03 per seed (labour only)	Negligible	Dependent on area needing protection. Small areas will be similar to seedling protection.	63 (caged) 393 (uncaged)
Seedling addition	2.00/seedling	0.67 per seedling	Additional $1.33 per seedling in labour; $3.40 per seedling in materials	15 (caged) 19 (uncaged)

4.4 Discussion

Is forest seed arrival increased by perches?

Perches failed as a stand-alone restoration tool in my study site. In the present experiment, no forest seeds were found, and I consider it most likely that almost none arrived. I acknowledge that absence of evidence is not evidence of absence of an effect. A different perch design or more seed traps may have led to forest seeds being detected around the perches. However, perches can only increase seed deposition where there are frugivorous birds; from the limited data available, and taking into account the absence of any bird activity on my trail cameras, frugivorous bird presence in the wetland was apparently low. In areas like ours attracting birds with perches will be difficult due to the lack of any fruit or other reward on perches; in other areas, the problem is likely to be that birds feed on early successional species in disturbed areas and disperse these seeds. I cannot rule out forest seed arrival in the perch seed traps because evidence of possums was found in all seed traps underneath perches and possums may have disturbed seeds that arrived. However, I consider this is unlikely: post-dispersal seed predation and removal of depulped seeds has been found to be very low in New Zealand (Moles & Drake 1999), and exclosure studies have found possums do not eat sufficient seeds to prevent the establishment of woody native seedlings (Jane & Pracy 1974b; Allen, Payton & Knowlton 1984; Stewart & Burrows 1989). At best, my findings demonstrate that seeds that did arrive under perches were at a greater risk of detection and predation, and if they established, herbivory, by possums once they have established.

Are perches a cost-effective restoration tool?

Perches are a (relatively: McDonnell and Stiles (1983)) novel restoration method. Planting seedlings is the most common restoration technique for increasing vegetation cover (de Souza Gomes Guarino & Scariot 2014). The application of seed to restoration areas ('direct seeding') is less commonly used than the planting of seedlings. It has been calculated as being cheaper (10-30 times cheaper than seedling addition per 100 seedlings (Cole *et al.* 2011)). This is counter-balanced by the fact not all seeds will germinate and survive to be seedlings (de Souza Gomes Guarino & Scariot 2014); survival rates are variable

(Cole *et al.* 2011) and therefore cost per seedling is variable. It has been tested successfully as a supplement to natural regeneration (Bonilla‐Moheno & Holl 2010), in abandoned pastures (de Souza Gomes Guarino & Scariot 2014). However it has been unsuccessful in early-successional species due to low quality seed and unseasonal dryness (Engel & Parrotta 2001). Seed predation and seedling herbivory can be prevented either by protecting seeds and seedlings from herbivorous species in situ with cages – which doubled seedling survival rates in restoration work: Sweeney, Czapka & Yerkes (2002), and also allows natural regeneration to occur: Jane & Pracy (1974); Allen, Payton & Knowlton (1984); Stewart & Burrows (1989) – or undertaking control work to reduce or remove herbivorous species (North, Bullock & Dulloo 1994). For small-scale restoration efforts it is likely to be cheaper to protect seed and seedlings through the use of exclosures than to undertake pest control which may need to be repeated as reinvasion occurs. To reduce costs of planting large areas, interest has arisen in restoring the process of dispersal to assist or 'kickstart' natural regeneration by planting small stands of trees, often termed 'applied nucleation' (Corbin & Holl 2012). These forest nuclei may increase *forest species seed deposition* (Reid, Holl & Zahawi 2014), and also forest species *establishment* through facilitation (Aide & Cavelier 1994; Holl 1999; de la Peña-Domene *et al.* 2014). Eventually, seedlings in disturbed areas will grow to form nuclei of regeneration (Corbin & Holl 2012), improving biotic conditions and may act as bird-attractants, potentially enhancing the seed rain of forest species from the surrounding area (Albornoz *et al.* 2013).

Perches, if effective, could provide an alternative method of applied nucleation. My seedling experiment has shown that it would cost $6.67 for each surviving forest seedlings to three years of age with herbivore protection. A perch with herbivore protection is estimated to cost $295, so based on current costings, a perch would need to produce more than 44 surviving seedlings attaining at least three years to be more cost-effective than planted seedlings. In a relatively harsh environment like the wetland and based on sowing experience (15.4% caged germination and survival), I estimate this would require approximately 285 viable seeds being dispersed under each perch. This is the economic reality of

perches: there are very few situations under which economic viability will be met.

A lack of cost effective forest species establishment is consistent with international experience, which has failed to demonstrate that perches increase the establishment of forest seedlings (McDonnell & Stiles 1983; McDonnell 1986; McClanahan & Wolfe 1987; McClanahan & Wolfe 1993; Aide & Cavelier 1994; Holl 1998; Shiels & Walker 2003; Zanini & Ganade 2005; Graham & Page 2012). Indeed, of the temperate studies commonly cited in favour of perches, McDonnell and Stiles (1983) found 93% of seeds dispersed were *Rosa multiflora*, which is not a forest species but considered to be an invasive weed (Banasiak & Meiners 2009) in the United States where the study was conducted; McClanahan and Wolfe (1993) found that between dispersal and germination, small seeded species became the dominant group; and later successional trees failed to establish; McDonnell (1986) found an increase in endozoochorus seeds, but seeds were typical of fields and forest edges, and over half the seeds were *Toxicodendron radicans* (poison ivy) or *R. multiflora* (above); and McClanahan and Wolfe (1987) did not test seedling establishment. These papers are often cited as evidence for the potential utility of perches without noting their limitations.

In an optimal situation, perches will be in areas close to forest fragments which continue to support abundant birds. In this situation, the cost per seed derived from perches will be low. However, this is also the situation where seeds are most likely to arrive even without perches. Density-dependant mortality will reduce some of the economic benefits of higher rates of seed deposition around perches, compared to anthropogenically dispersed seeds, which can be dispersed at more suitable densities by hand (small scale) or helicopter (large scale). The benefits of nucleation are not unique to perches. Mature trees will provide fruit to attract birds and facilitate dispersed seedlings (e.g. shade) in ways perches cannot. Simple adjustments to spatial planting arrangements can achieve regeneration in nuclei, in less time and with greater certainty, as seedlings can be planted and birds are not relied upon to visit.

4.5 Conclusions

Restoration of forest in non-forested areas entails addressing more constraints than seed limitation, which is the only constraint perches may address. My results have demonstrated that direct seeding is a more cost effective means of obtaining many, smaller seedlings than perches, but that seed predation and herbivory will halve survival. Seedling addition is also more cost effective than perches, but plants are larger and more resistant to herbivory once planted, compared to sown seeds.

Given that the benefits of perches are not unique and can be achieved with greater certainty and less cost through other methods, why persist with the folly of perches? Perches are charismatic and novel and certainly capture the public's imagination more than plant and release methods. However, they appear to be largely answering the wrong question – seed arrival, not seedling establishment. The benefits and costs of bird perches for forest restoration should only be considered in light of the complementary methods required to make them viable, and competing methods which are cheaper and provide more certainty of restoration success. I have found perches will rarely address the rate-limiting step to forest regeneration in a temperate setting and even where dispersal limitation exists, direct addition of seeds or seedlings is likely to be substantially more cost-effective.

Chapter Five: Successional engineering: is *Chionochloa rubra* a suitable nurse species for native forest?

5.1 Introduction

Biotic interactions affect the degree to which plant species may establish in new environments. Negative interactions with other plant species occur as a result of competition (for space; water; nutrients; or light) (Goldberg & Barton 1992) or inhibition (allelopathy) (Muller 1969). Positive interactions (facilitation) include interactions such as buffering from harsh environmental conditions (Belsky 1994), protection from herbivory (Brown & Ewel 1987; García & Obeso 2003), or making conditions more favourable, such as nitrogen fixation (Bonanomi, Incerti & Mazzoleni 2011). The use of nurse species in restoration has been shown to increase the success of reforestation, but this effect varies depending on the environment and species (Castro *et al.* 2004; Gómez-Aparicio *et al.* 2004).

I set out to compare the differential performance as nurse species of a native New Zealand tussock species and *Leptospermum scoparium* (mānuka) a recognised forest regeneration facilitator (Ogden & Stewart 1995). Although mānuka is a native tree and can be considered a component of native forest, I refer to later successional, broadleaf-podocarp forest in this chapter as native forest, and refer to mānuka by its name. Mānuka follows tussock species in successions (Rogers & Leathwick 1994), and therefore successful forest restoration into tussock would allow faster native forest regeneration by skipping a successional stage.

Tussock grassland species in New Zealand appear suitable for forest species invasion in appropriate areas, if not facilitators thereof. Prior to anthropogenic disturbance, grasslands, including *Chionochloa* species, were restricted to areas above the tree line, or in areas where forest could not grow: wetlands, areas of poor soils, and dry intermontane basins (McGlone 2001). Grasslands expanded beyond their pre-human habitat range as early successional species following human settlement and disturbance, and within them, tall tussock (*Chionochloa*) species became more dominant (Rogers 1994, McGlone 2001, O'Connor 1984). Anthropogenic fire has been the dominating influence on the relative distribution of forests and tussocks on eastern New Zealand over the past 1000 years (Molloy *et al.* 1963; McGlone 1983; McGlone 1989). *Chionochloa* are now vulnerable to displacement by agriculture and forestry (Rose, Platt & Frampton 1995) and invasion by exotic species (Treskonova 1991). Recent losses of tussock grasslands nationwide and within the Southland region over the past 20 years are primarily attributable to commercial exotic forestry plantations (Figure 5.1).

Chionochloa rubra, my study species, is a tall tussock species endemic to New Zealand and has a wide environmental tolerance, forming grasslands on damp, leached soils (Wardle 1991). In environmentally suitable areas it is invaded by *Dracophyllum* species, mānuka and *Kunzea ericoides* within a 45-55 year time period following disturbance (Rogers & Leathwick 1994), and predicted to subsequently reach native, later-successional forest within two to three centuries.

Awarua wetland, New Zealand's oldest and largest Ramsar convention-recognised wetland, contains approximately 10,000 ha of mānuka (Anon. 2010) and low levels of forest regeneration. Mānuka is an example of time-dependent nurse species suitability: suitability increases as it ages, with an initial high density of stems being resistant to invasion (Esler & Astridge 1974). Growth rates are site-specific, however Esler and Astridge (1974) suggest mānuka begins to self-thin around 15-20 years, but can continue to grow slowly for up to

50 years, reaching a maximum height of 12 m before being replaced. Sites measured within the wetland complex had mean ages ranging from 29 to 34 years (based on tree-ring aging, see Chapter Two for details), but were considered to have a slower growth rate than that discussed in Esler and Astridge (1974). Average heights in Awarua wetland ranged from 3.2 to 5.5 m, whereas by 20 years Esler and Astridge (1974) suggest mānuka will reach 7 m. Areas mapped several years ago as *C. rubra* communities have been observed subject to on-going invasion by mānuka, meaning that if forest can be established in these, a substantial forest delay (perhaps 100 years or greater: refer Esler (1967), Wilson (1994), and Allen *et al.* (1992)) can be avoided. Tussock species are highly flammable due to the accumulated dead biomass of leaf bases and sheaths. Tussock and mānuka cover increase the flammability of landscapes relative to forest (Ogden, Basher & McGlone 1998), therefore speeding regeneration to forest would both increase the amount of forest habitat within the region and also reduce the flammability of the wetland.

The aims of this study were to:

(1) Test whether forest species sown as seeds and planted as seedlings in native tussock *C. rubra* would germinate, survive and grow;

(2) Compare the germination and growth of sown seeds and planted seedlings in *C. rubra* to seed as well as seedling germination and growth in the recognised nurse species of mānuka;

(3) Compare the relative effects of environmental facilitation and facilitation in the form of protection from herbivory, by analysing whether the effects of caging differentially affected seeds and seedlings in *C. rubra* and mānuka;

(4) Quantify whether seed and seedling survival and growth is correlated more with environmental conditions or the habitat type, by testing against environmental variables that have a similar range for both nurse species.

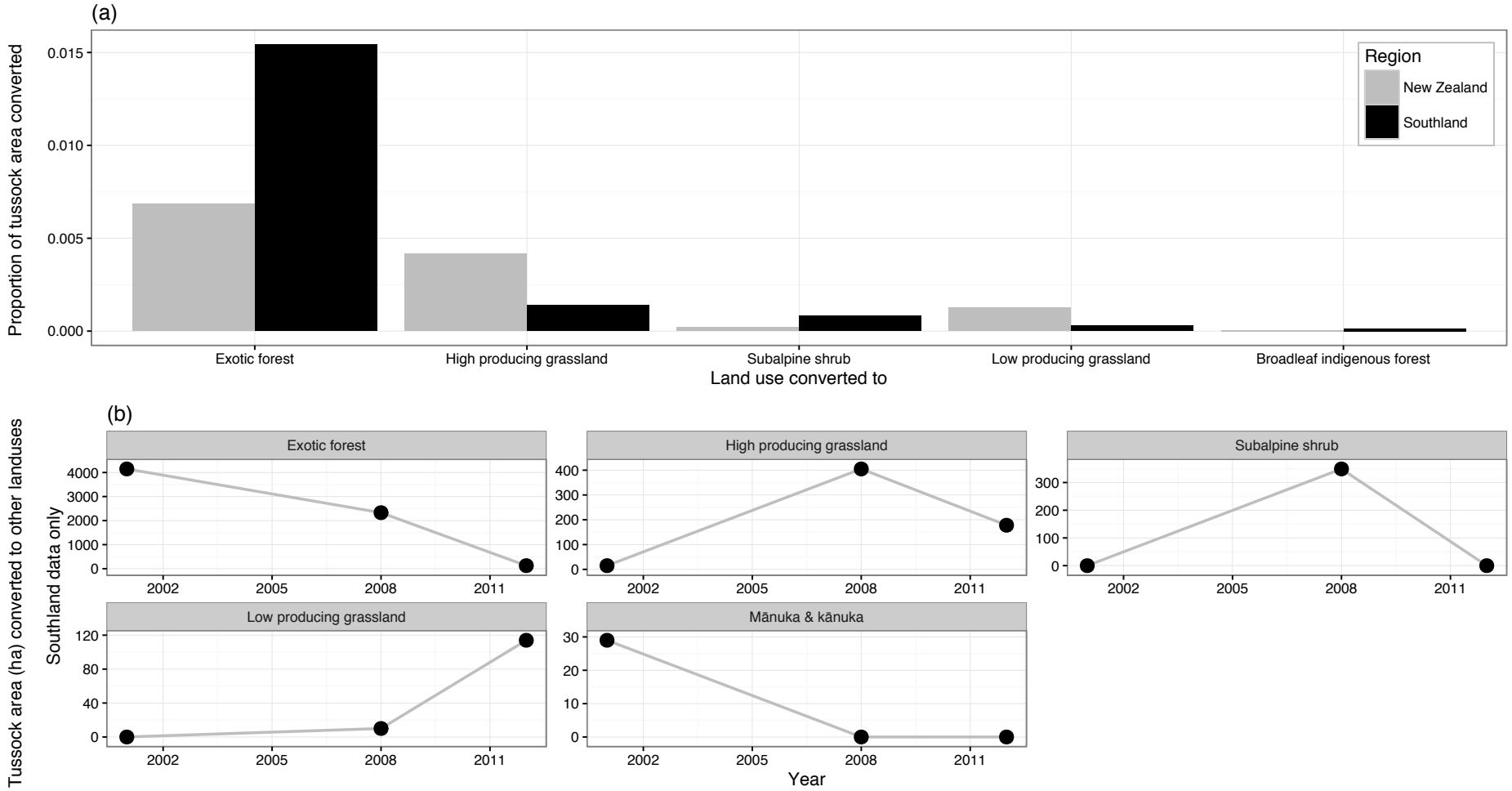


Figure 5.1: Causes and rates of loss of tussock grasslands to other land use types (source: LCDB v4.1). (a) Proportion of pre-existing tussock area in 1996 converted to other land uses by 2012, for New Zealand overall (grey bars) and the Southland region (black bars). (b) Rates of conversion to other land uses over the period 1996 – 2008 for the Southland region. Area is shown in hectares. The five most common converted-to land use types are shown (top row: exotic forest, high producing grassland, subalpine shrub; bottom row: low producing grassland and mānuka and kānuka combined).

5.2 Methods

The experimental work was undertaken within the Awarua Ramsar wetland catchment (Figure 5.2), in Southland, New Zealand.

According to a combination of aerial photos and ground-truthing (Anon. 2010), the wetland catchment contains more *C. rubra* communities mapped than is recorded in the LDCB for all tussock vegetation types combined. Although there is no time series of this higher resolution data which was published in 2010 and used 2008 aerial mapping, it was apparent in site selection that some sites had been invaded by mānuka subsequent to mapping and others were in the process of mānuka establishment.

Site selection

I selected 10 sites that had been mapped as *C. rubra* communities (Anon.) for investigation as potential sites. Landowner permission and safety concerns restricted access to two sites; two further sites had been invaded by mānuka and were discarded. I chose six sites in mānuka as controls for the remaining six tussock sites (Figure 5.2). Hereafter, because certain environmental variables (amount of light available, pH) co-varied with nurse species, I will use the term 'habitat type' to differentiate between the control (mānuka) and treatment (*C. rubra*, or 'tussock') sites.

At each site I set up a sowing experiment for seeds, and seedlings (hereafter termed 'plants' to avoid confusion between seeds which germinated into seedlings, and plants that were seedlings at time of planting).

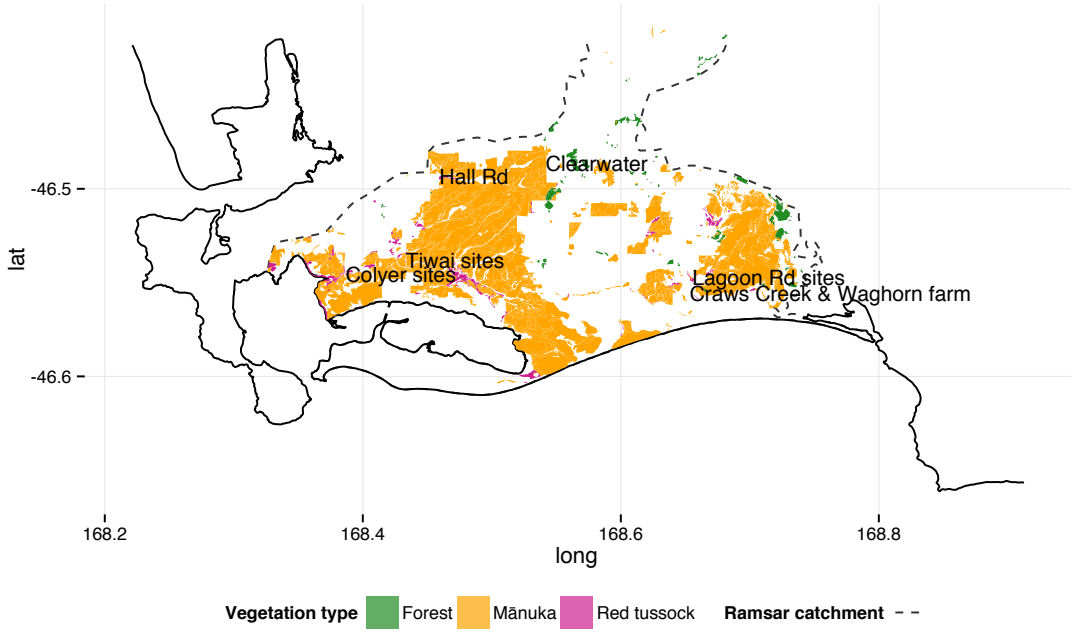


Figure 5.2: Experimental sites for forest seedling addition. The yellow shows areas mapped as mānuka in the wetland, the violet, areas mapped as *C. rubra* and the green, indigenous forest. One site was established at Hall Rd, Clearwater, Craws Creek and the Waghorn farm site. Three sites were established at Tiwai (two in mānuka, one in tussock), two at Colyer Stream (one in mānuka, one in tussock). Three sites were established adjacent to Lagoon Rd (two tussock, one mānuka).

Experimental setup and measures

Sowing experiment

At each site I tested seed germination and survival by sowing 100 seeds of three species that had been locally sourced within the wetland (*Pseudopanax crassifolius* (n = 40), *Pittosporum tenuifolium* (n = 20) and *Aristotelia serrata* (n = 40)), in both caged and uncaged replicates. Seeds were sown over four days (28 – 31 October 2013). To prevent seeds rolling away I used 4 cm wide strips of lexan polycarbonate (1 mm thick) with the ends stapled together to construct 10 cm diameter tubes. Tubes were inserted into the soil approximately 50 cm apart with around 2 cm of the tube remaining above ground. I constructed 20 cm high mammal-proof cages using 5.8 mm aperture stainless steel weldmesh. Cages and tubes were secured to the ground with wire pegs.

Seedling emergence and survival was measured on three occasions: 1-2 March 2014, 8-9 May 2014 and 10-12 December 2014. All results are presented as the number of seedlings that have emerged and are alive as a percentage of the total number sown. I did not measure heights of seedlings. At the time of sowing and at each remeasure (above) I also measured environmental variables.

Environmental variables

The environmental variables at sites measured at the time of establishment and each site visit thereafter were depth to groundwater, soil moisture and soil conductivity. Soil moisture (%) and soil conductivity (mV) were measured using a Delta-T soil moisture meter, which measures soil moisture content by responding to changes in the apparent dielectric constant of moist soil. Depth to groundwater was measured by digging until groundwater was reached, left to reach equilibrium and then depth from the soil surface to water surface was measured. Soil samples were collected in April 2014 over a period of two days using a standard 10 cm diameter, 10 cm deep soil core, bagged, sealed and stored in an insulated container until all had been collected, after which they were sent immediately to Landcare Research New Zealand Ltd environmental chemistry lab in Palmerston North who measured the following parameters: dry bulk density, water content (% of dry weight), pH (1:5 water), electrical conductivity (dS/m), organic carbon (%), total nitrogen (%), carbon-nitrogen ratio, total P (mg/kg). Leaf litter was removed from the ground surface prior to soil sampling.

Planting experiment

At each site I planted three species (*P. crassifolius*, *P. tenuifolium* and *M. lanceolatus*) over the period 23 – 31 October 2013. Plants were grown from locally sourced seed (seeds were locally sourced from forest remnants within 30 km of Awarua) at Pukerau Nurseries, Southland. Species were planted separately in caged and uncaged replicates, for a total of six replicates (two-level caging treatment multiplied by three species) at each site. Caged and uncaged replicates contained five plants for *P. crassifolius* and *P. tenuifolium*. Each caged and uncaged replicate of *M. lanceolatus* contained 4 plants. Plants were spaced

equally for both caged and uncaged subplots. Subplots were located amongst red tussock, in areas with sufficient space between plants to allow for the subplot to be established. Each plant was tagged with a unique identifier to allow for repeated sampling. Cages were constructed of 'KBC Handy Mesh', a UV-stable plastic 10 mm mesh, supported by metal fencing stakes and secured to the ground with wire pegs (see Figure 5.3).

Heights were measured immediately upon planting, and then remeasured on four occasions: 6-7 December 2013, 1-2 March 2014, 8-9 May 2014, 10-12 December 2014, from the ground to the uppermost living leaf tissue to avoid counting dead stem matter following herbivory events.

Plants were removed in the December 2014 remeasure after 13 months of growth in-situ, weighed, dried in drying ovens at 60° C until water loss ceased and then re-weighed to measure dry biomass per plant. Plants were removed at ground level, so biomass measures exclude any root-weight.

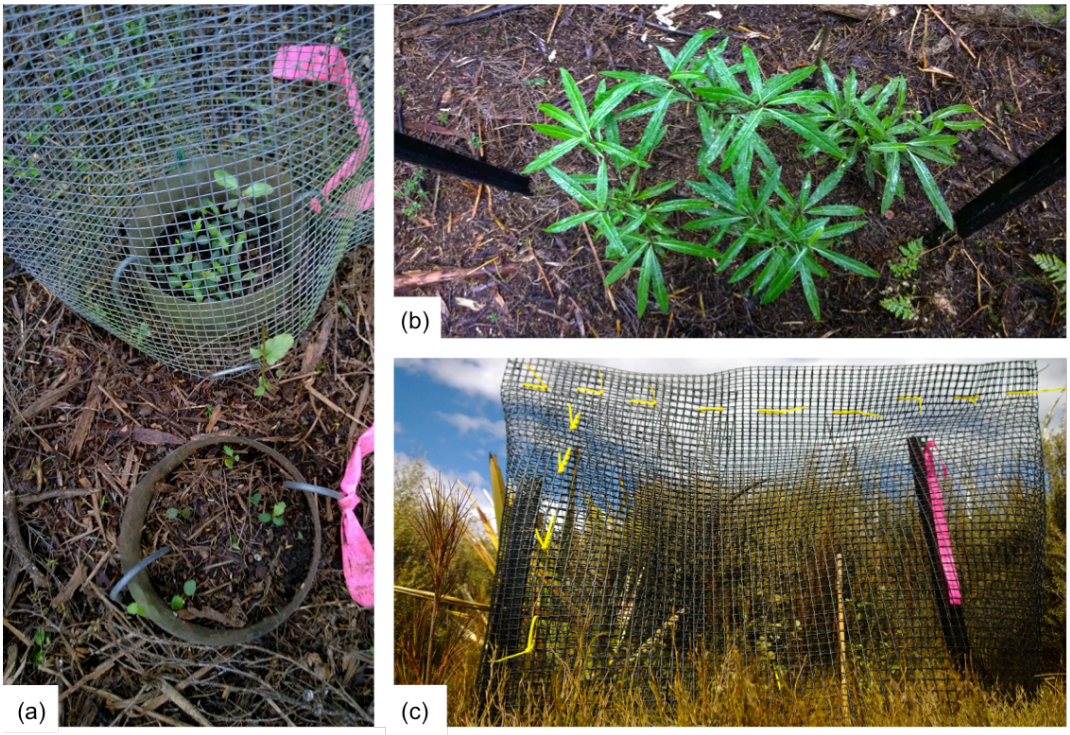


Figure 5.3: (a) Germination experiment set up - caged and uncaged. (b) Planted *M.lanceolatus* plants (caged, cage temporarily removed for measurement), taken May 2014. (c) Constructed plant cage with *C. serratus* plants inside, taken November 2013.

Analysis

All statistical analyses were undertaken using the statistical software programme R (R Core Team 2015).

Sowing experiment

I analysed germination and survival of *Pseudopanax crassifolius* only due to low germination of *Pittosporum tenuifolium* and *Aristotelia serrata* (see Results).

I used a generalised linear mixed effects model from package LME4 (Bates *et al.* 2014), with a binomial error distribution to quantify statistically germination and establishment (expressed as a proportion of total seeds sown) and the effect of caging over time, for mānuka and tussock habitat types separately. I used a random intercept for each site (n = 12) that contained one caged and one uncaged replicate, each sown with 40 *P. crassifolius* seeds.

I compared the effect of habitat type and caging using a generalised linear mixed effects model (function `glmer` from package LME4) with a binomial distribution. The response was in the form of total established as at December 2014, minus the total sown in each replicate (n = 40). I used a nested random intercept term of caging treatment (n = 2) within each site (n = 12), providing a total of 24 intercepts for the random effects. This kind of random effect specification is called explicit nesting, and is functionally the same as implicit nesting, which in this case would involve giving each site a unique identifier, and each replicate a unique identifier, and specifying a random intercept for both.

I tested the importance of environmental impacts on seed germination and seedling survival by running multi-model selection using package MuMIn (Bartoń 2014) in R. I calculated the variable importance for the subset of models for which delta AICc was < 4. The global model model selection table and model-

averaged full coefficients (adjusted for parameter shrinkage) are provided in Appendix 5.1.

Planting experiment

Plant survival for two of the three species, *M. lanceolatus* and *C. serratus*, was analysed with a generalised linear mixed effects model using package LME4, with a binomial error distribution, a random intercept for location (n = 12) and a random slope for species. Survival rates in *P. tenuifolium* were too high to analyse effectively statistically due to data separation (i.e. zero variation in some treatments).

I measured plant growth and health by recording change in height (height from base of stem in ground to tip of living tissue) between sowing (October 2013) and harvesting (December 2014). I used a generalised linear mixed effects model to quantify the effect of habitat type and caging on mean seedling height change ratio (height at end of experiment divided by the initial height, for each plant) with replicate as the unit of replication. I quantified the importance of nutrient and groundwater gradients (carbon-nitrogen ratio, mean depth to groundwater, a second-order polynomial term for mean depth to groundwater, coefficient of variation in mean depth to groundwater) using a set of candidate models. I used a polynomial term for groundwater to test for a non-linear response to the environment (e.g., sites might negatively affect growth if they were too wet or too dry). Model-averaged coefficients were derived from models with delta AICc < 4. All models had a Gaussian error distribution. I used package GLMMADMB (Skaug *et al.* 2014) to run the Gaussian models.

Environmental variables

I tested whether environmental conditions differed between habitat type using multivariate analyses. I used Hellinger-transformed data and Euclidean distance in all analyses. I performed a permutational anova to check whether the habitat-type groups differed, and an analysis of dispersion comparing the average distance from each site to its centroid. The sites (with environmental parameters used as 'species' in the traditional sense) were ordinated using non-

metric multidimensional scaling, an indirect gradient analysis approach. Based on the ordination I calculated the 95% confidence ellipse around each habitat type's centroid. All multivariate analyses were undertaken using the package VEGAN in R (Oksanen *et al.* 2013).

5.3 Results

Early-stage establishment: sowing experiment

No seeds of *Aristotelia serrata* germinated in mānuka and the maximum seen across all plots in tussock was 4 (caged) and 2 (uncaged), and therefore this species has been excluded from statistical analysis. In any one count the maximum number of germinated *Pittosporum tenuifolium* seedlings seen was three (across all plots), and therefore this species was also excluded from further analysis.

Total *Pseudopanax crassifolius* seedlings in tussock continued to increase over the 13 months of observation inside cages, with 15% established 6 months post–sowing and 22% surviving at end of experiment (Figure 5.4). Outside cages seedlings increased initially and then decreased to 5% surviving. The difference between time periods was significant only between April 2014 and December 2014 ($z = 2.172$, $p = 0.03$). The protective effect of caging was only significant in the December 2014 measure ($z = 3.740$, $p < 0.001$).

In mānuka, caged *P. crassifolius* reached maximal germination in May 2014 (36%), six months after sowing. Uncaged *P. crassifolius* never reached the same total and continued to decrease following the first measurement. As with tussock habitat types, the protective effect of caging was only significant in the December 2014 measure ($z = 2.030$, $p = 0.04$). Raw results are provided in Appendix 5.1.

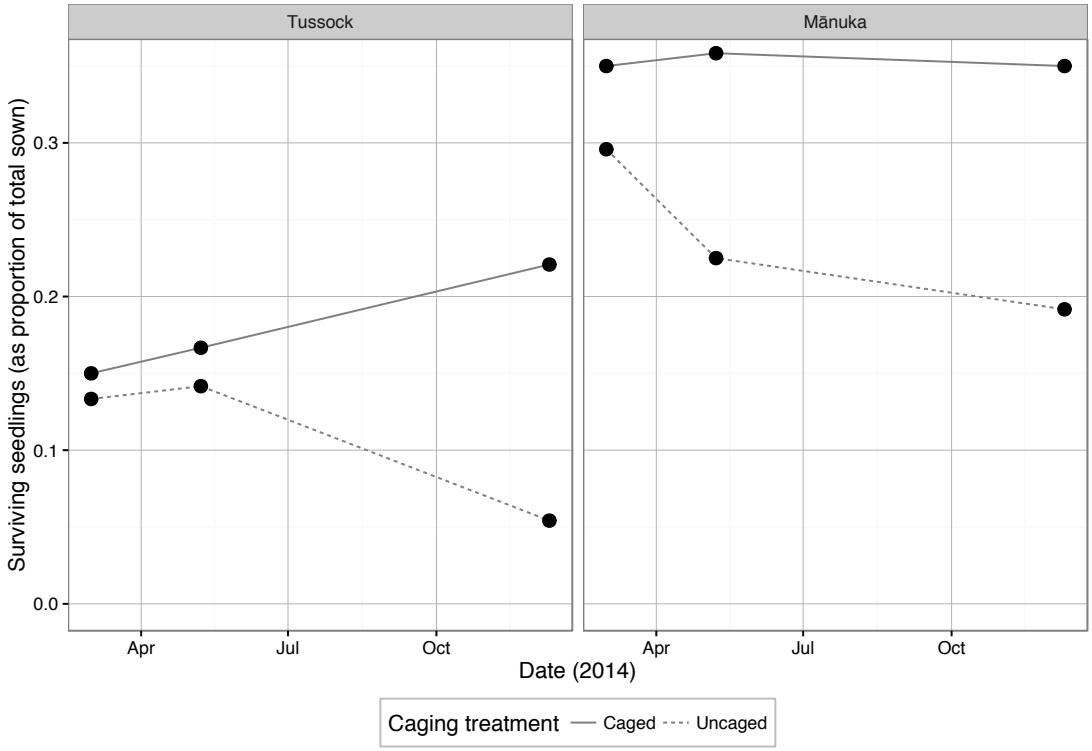


Figure 5.4: *Pseudopanax crassifolius* sown seed germination and establishment over one year. Seeds sown in November 2013.

By the end of the experiment in December 2014, the proportion of established seedlings was significantly higher under both habitat types with protection from herbivores and seed predators (caging: z = 1.960, p = 0.050, Figure 5.5(a)). Fewer seedlings survived in tussock, and a lack of caging was more detrimental in tussock areas (Figure 5.5(a)), but neither effect was significant (effect of tussock as a nurse species: z = -1.251, p = 0.211, effect of uncaged, tussock as a nurse species: z = -0.946, p = 0.344).

I tested the relative importance of natural environmental gradients against our treatments using the Information-Theoretic Model Comparison approach (Burnham & Anderson 2002). Models were compared using Akaike's Information Criterion for small sample sizes (AICc) which maximises fit to the data while penalising overfitting; delta AIC indicates the difference between the 'top' model and subsequent models. I selected the subset of models with delta AICc < 4 (Burnham & Anderson 2002) and tested the importance of variables by calculating the sum of the Akaike weights for models containing each variable (see model selection table in Appendix 5.2). Caging treatment was the most

important of all variables tested (appearing in all models in the subset) with a relative importance of 1, followed by habitat type which had a relative importance of 0.49, and the ratio of carbon to nitrogen which had a relative importance 0.15 (Figure 5.5(b)). A summary of the model-averaged coefficients is presented in Appendix 5.3.

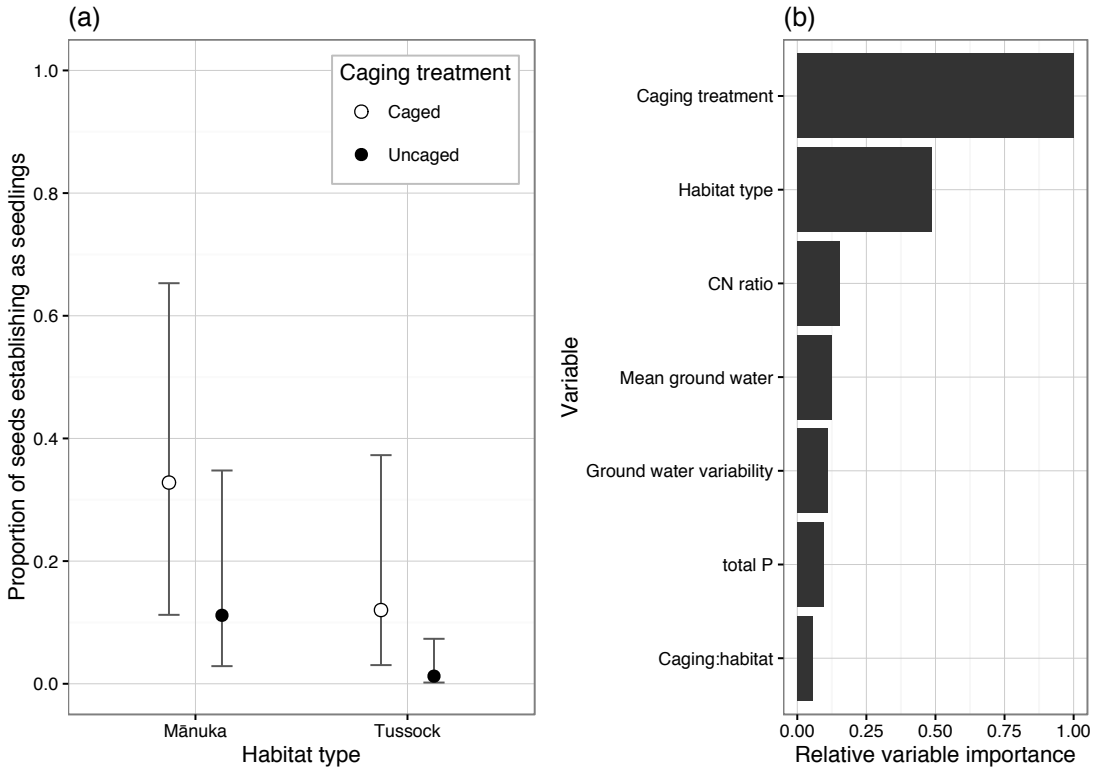


Figure 5.5: (a) Modelled treatment effects of habitat type and caging on *Pseudopanax crassifolius* germination and survival, error bars indicate 95% confidence intervals. The difference between caging treatments is significant only, but all modelled main and interaction effects are shown. (b) Seed germination and survival model selection relative variable importance (based on subset of models with delta AICc < 4).

Middle-stage establishment: Planting experiment survival and growth

Looking at survival of nursery-grown plants, I found a significant, species-specific interaction between caging and habitat type. Planting seedlings in tussock areas negatively affected survival rates (relative to mānuka areas) in uncaged *M. lanceolatus.* ($z = -1.982$, $p = 0.048$), and had a negative but non significant effect on both caged and uncaged *C. serratus* (Figure 5.6). Survival rates in *P. tenuifolium* were too high to analyse effectively statistically due to data separation. Full survival data is provided in Appendix 5.4.

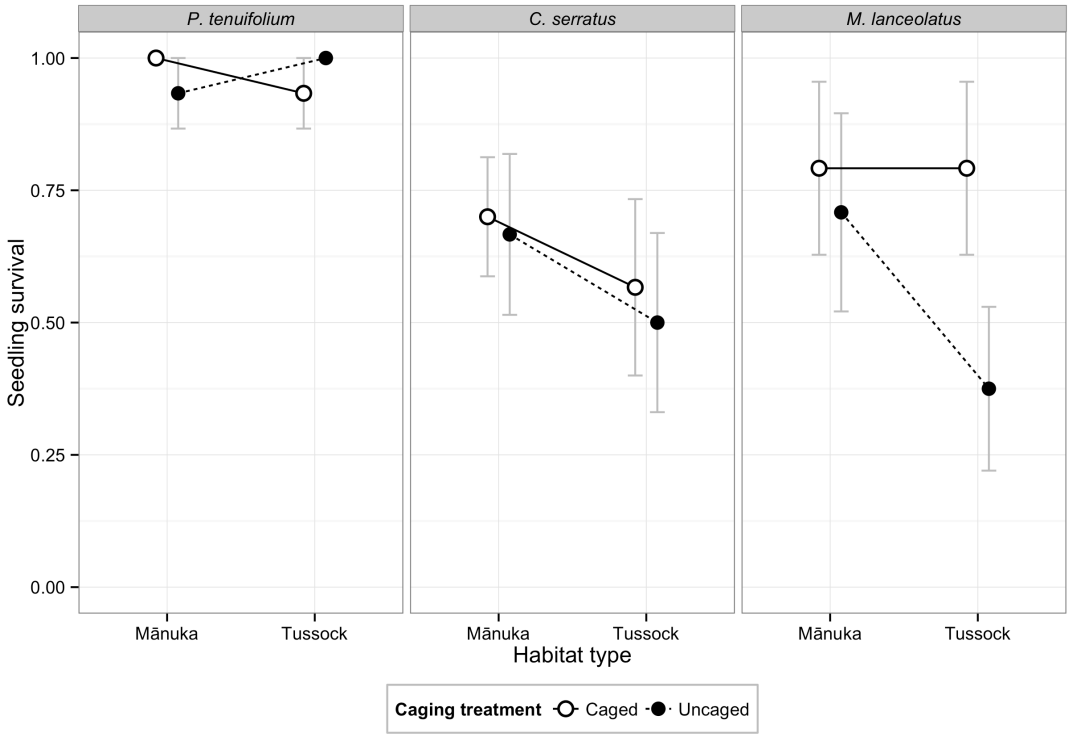


Figure 5.6: Seedling survival (mean) for *P. tenuifolium*, *C. serratus*, and *M. lanceolatus* under habitat type and caging treatments, as a proportion of number sown. Errorbars show standard error around the mean.

Although very few seedlings died, 18% (n = 22) of *C. serratus* seedlings and 14% (n = 13) of *M. lanceolatus* seedlings failed to thrive and ended the experiment at less than or equal to 30% of their initial starting height (Figure 5.7). This led to a zero-inflated, overdispersed distribution, and so I chose to model growth as a two-step process (a 'hurdle model' approach, where binary outcomes [dead and shrunken vs healthy] are modelled separately to the continuous response (Aitchison 1955)). The results of the binary analysis (whether a seedling's growth ratio exceeded 0.3) were consistent with the survival analysis (whether a seedling survived) and therefore I only present the second stage of the analysis, the analysis of the heights for those seedlings that exceeded a growth ratio of 0.3. The raw means for all seedlings (including with those with a growth ratio of ≤ 0.3) are shown in Figure 5.8.

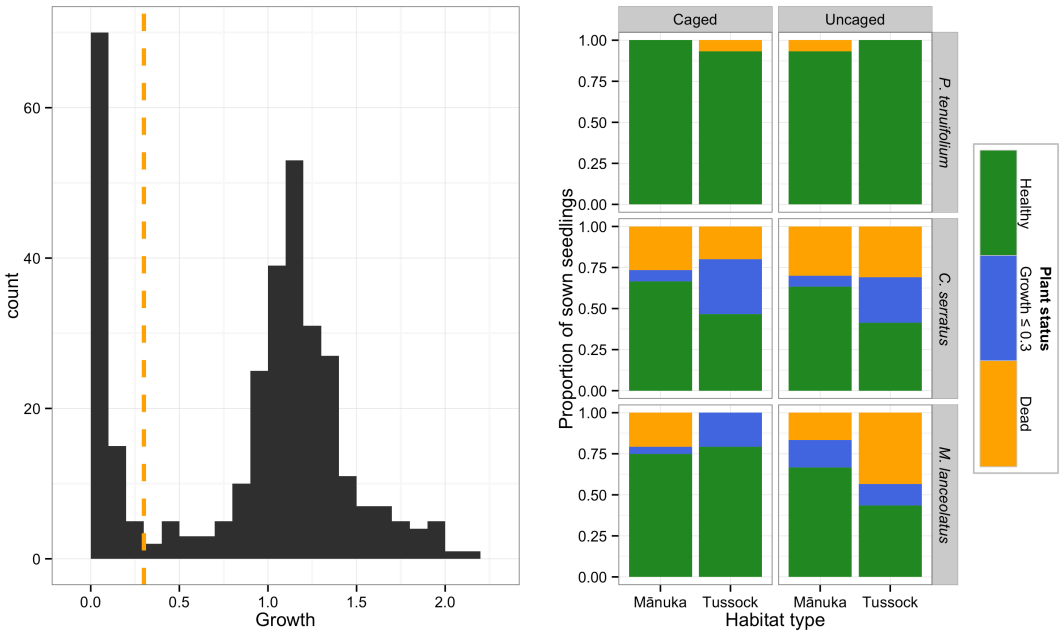


Figure 5.7: Left, plant growth (end of experiment height/initial height), demonstrating a bimodal distribution. Binwidth is 0.1. Dashed orange line indicates growth - 0.3, i.e., plants were 30% of their starting height at the termination of the experiment. Plants with a growth ratio of ≤ 0.3 were excluded from the heights analysis. On the right, the relative proportions of healthy, plants with a growth ratio of ≤ 0.3 and dead plants for each species by habitat type and caging treatment.

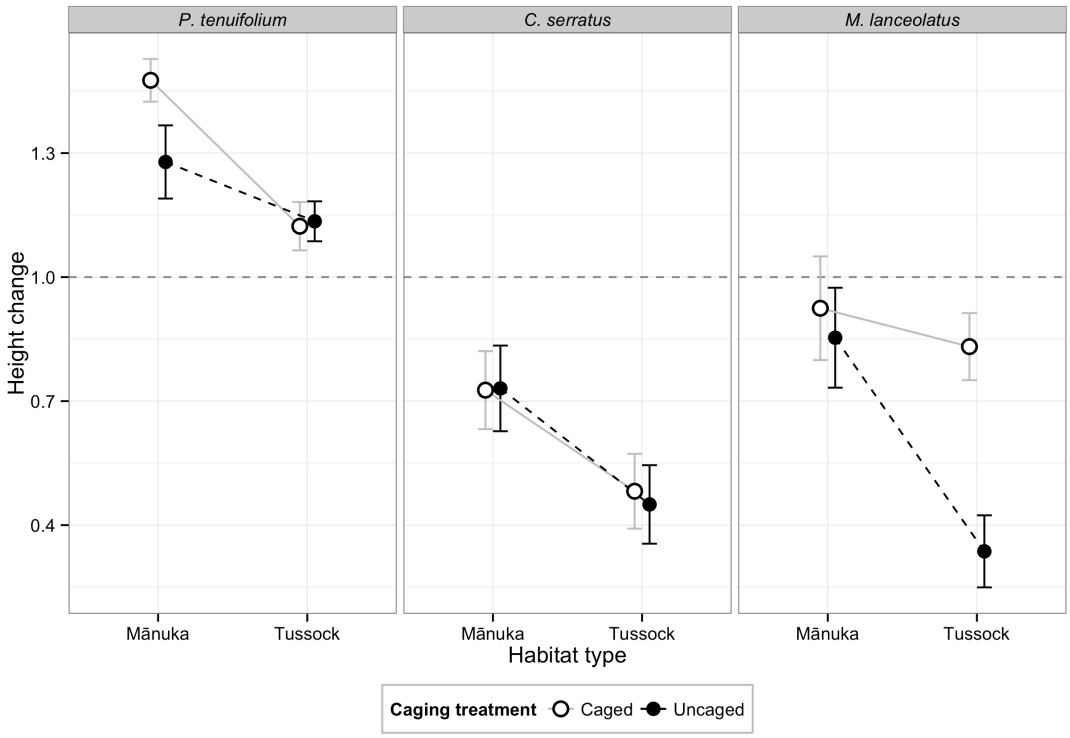


Figure 5.8: Planting experiment - mean change in plant heights: summarised raw data prior to exclusion of plants with a growth ratio of ≤ 0.3. Values are the mean for each treatment of height at

end of experiment divided by height at the beginning of experiment for each seedling, with error bars indicating standard error around the mean.

P. tenuifolium seedlings grew significantly more than *M. lanceolatus* (z = 2.44, p = 0.015) and *C. serratus* (z = 4, p < 0.001) seedlings, and grew significantly less in tussock ecosystems (z = -2.36, p = 0.018). The effect of tussock was negative but not significant for *C. serratus* and *M. lanceolatus* (z = -0.21, p = 0.83 and z = -1.51, p = 0.131 respectively), although excluding seedlings with a growth ratio of 0.3 reduced the number of samples for these species (Figure 5.7).

Table 5.1: Full results from seedling heights analysis, using a generalised linear mixed model. Reference condition is *P. tenuifolium*, caged, in mānuka habitat. Species codes are as follows: CARSER – *Carpodetus serratus*; MELLAN – *Melicytus lanceolatus*; PITTEN – *P. tenuifolium.*

Variable	Estimate	SE	z value	Pr(>|z|)	
(Intercept)	1.48	0.08	17.58	< 0.0001	***
Habitat: tussock	-0.28	0.12	-2.36	0.018	*
Caged: uncaged	-0.13	0.09	-1.32	0.186	
Species: CARSER	-0.43	0.11	-4	< 0.0001	***
Species: MELLAN	-0.26	0.11	-2.44	0.015	*
Habitat: tussock : Caged: uncaged	0.07	0.13	0.49	0.626	
CARSER : tussock	0.12	0.16	0.77	0.444	
MELLAN : tussock	0.03	0.15	0.23	0.821	
CARSER: uncaged	0.21	0.14	1.45	0.148	
MELLAN: uncaged	0.09	0.15	0.57	0.568	
CARSER: tussock, uncaged	-0.05	0.21	-0.21	0.830	
MELLAN: tussock, uncaged	-0.32	0.21	-1.51	0.131	

I tested the relative importance of natural environmental gradients against our treatments using the Information-Theoretic Model Comparison approach (Burnham & Anderson 2002). I included full interactions of my manipulated treatments and a number of ecologically explainable environmental variables and a subset of their interactions. I discarded pH, as pH in mānuka ranged from 4.29 – 4.48 while tussock ranged from 4.51 – 5.15 (no overlap), and therefore might have acted as proxy for variables that also diverged between the habitat

types. These values for pH are within normal bounds for bogs and swamps (Johnson & Gerbeaux 2004).

I selected the subset of models with delta AICc < 4 (Burnham & Anderson 2002) and tested the importance of variables (variable importance in Appendix 5.5, model selection table in Appendix 5.6, and model summary for model averaged coefficients are provided in Appendix 5.7). The most important environmental variable and only one selected in the delta AICc < 4 model subset was a non-linear effect of depth to groundwater (Figure 5.9). Increased is most rapid in wet soils (smaller depth to groundwater) but plateaued in drier areas. The prediction interval for *C. serratus* seedlings is shorter because no seedlings survived with a growth ratio of > 0.3 in the wetter plots (mean depth to groundwater < 21 cm). The only significant effect in the analysis was that *P. tenuifolium* seedlings had a higher growth ratio than *C. serratus* ($z = 4.852$, $p < 0.001$), or *M. lanceolatus* ($z = 3.035$, $p = 0.002$).

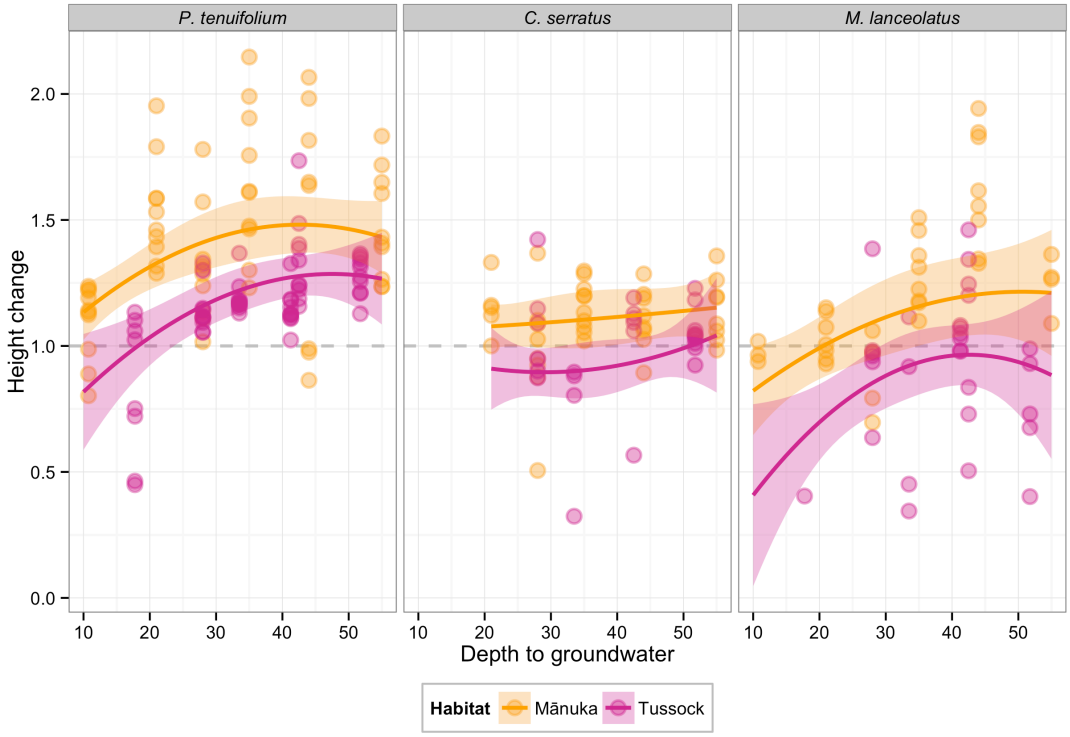


Figure 5.9: The predicted effect of depth to groundwater on planted seedling growth, planting experiment. Predictions (with 95% CI indicated by shaded area) are truncated to the range of raw data, which is shown on the plot – each point is the growth ratio of an individual seedling. *C. serratus* had no individuals surviving with a growth ratio of > 0.3 in areas where the mean depth to

groundwater was < 21 cm, hence the truncated predictions. The drier a site is (the greater the depth to groundwater), the height gain from start to end of experiment increases.

Plant biomass

I analysed biomass (weight in grams) as the sum biomass per replicate separately for each species. I found no significance difference in biomass between treatments, except for a significantly negative effect of being uncaged in tussock habitat types for *C. serratus.* I consider this is likely because the majority of the mass was made up of stem weight rather than leaf weight and seedlings were planted at two and three years age. Summarised raw data, model output and visualisation are included in Appendix 5.8.

How different are the environmental niches of tussock and mānuka?

Habitat type was not a significant predictor of the environmental niche of our sites ($F = 1.1975$, $DF = 1$, $R^2 = 0.11$, $p = 0.3$). Tussock sites were more diverse than mānuka sites (average distance to centroid: mānuka = 0.097, tussock = 0.100), but this difference was not significant ($F = 0.03$, $DF = 1$, $p = 0.87$). As already noted the mānuka sites were all more acidic than the tussock sites. The ordination suggests that mānuka sites vary more in terms of their groundwater gradients, while tussock sites vary more in their nutrient enrichment and variability in soil moisture and conductivity (Figure 5.10).

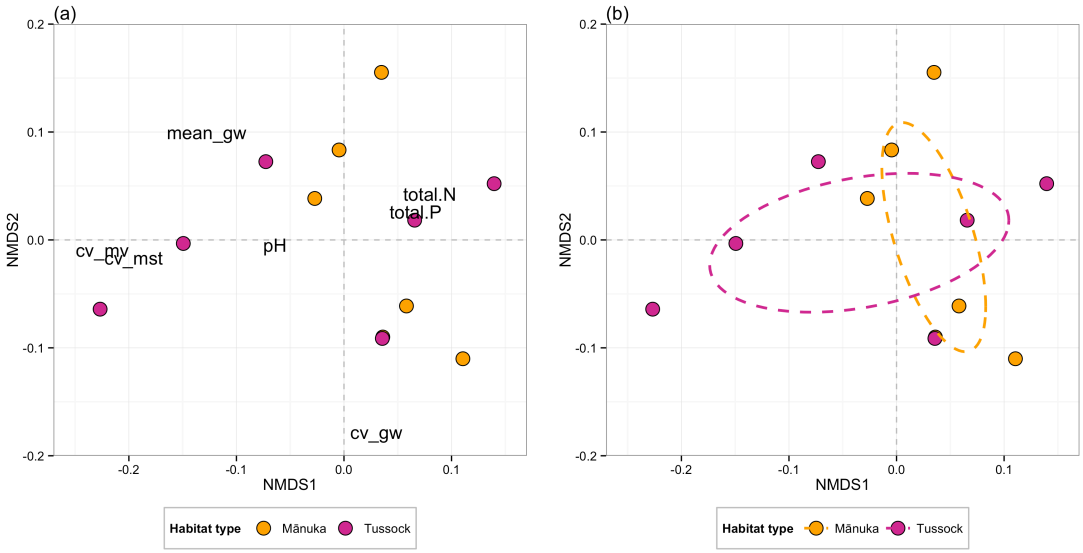


Figure 5.10: Results of ordinating sites based on their environmental variables. (a) Environmental variable centroids in text. Mānuka sites separate along the vertical axis, driven more by mean depth to groundwater ("mean_gw") and variability in depth to groundwater ("cv_gw"). Tussock sites separate along the horizontal axis, with sites higher in nutrients ("total.N" – total nitrogen; "total.P" – total phosphorus) to the right of the diagram and those with higher variability in conductivity and soil moisture ("cv_mv" and "cv_mst", respectively) to the left. (b) 95% confidence interval ellipse around habitat type centroids.

I did not measure canopy openness at my sites. The tussock is naturally shorter than mānuka and was observed to provide much less shade than mānuka. Seedlings in tussock were observed to be sun-stressed with yellower leaves and leaf spotting (Figure 5.11).

Figure 5.11: From left to right: *M. lanceolutus* in tussock, *M. lanceolatus* in manuka, *P. tenuifolium* in tussock, *P. tenuifolium* in manuka. All photos taken April 2014.

5.4 Discussion

The first two questions I addressed were whether seeds and planted seedlings in areas dominated by native tussock (*C. rubra*) would germinate, establish and grow, and how this compared to seeds and planted seedlings mānuka dominated areas. Seeds germinated and planted seedlings survived and grew successfully in tussock habitat types, fulfilling the first question. Overall, seed germination and planted seedling survival and growth was higher in mānuka, but choice between the two habitats is likely to be driven by other considerations, such as the age of mānuka and time to senescence.

I found that too few seeds of *Pittosporum tenuifolium* and *Aristotelia serrata* germinated in tussock or mānuka to analyse. These seeds showed higher viability in the wetland in Chapter 2 (5% germination and survival for caged *A. serrata*, 34% for *P. tenuifolium*). I consider the depressed germination and survival compared to Chapter 2 is more likely due to the length of storage of the seeds, which were refrigerated from collection in 2011 until sowing in December 2013, than environmental unsuitability. The same seeds were used in the sowing experiment in Chapter 2, but were sown within 2 months of collection. One plant species did germinate well despite the long storage and allows comparision between habitats. Seeds of *Pseudopanax crassifolius* germinated more slowly in tussock than those within mānuka; the mean effect size of caging seedlings was larger in tussock than in mānuka. The survival of *P. crassifolius* seeds was more correlated with the treatment effects of caging (relative importance: 1) and habitat (relative importance: 0.49) than with natural environmental gradients like depth to groundwater. In terms of restoration potential, while mānuka was a better nurse species, the mean effect size was modest (caged mānuka = 35% survival; caged tussock = 22% survival), given the low cost of seeds as a restoration tool (Engel & Parrotta 2001; Cole *et al.* 2011).

Planted seedling survival was high for all species, in both tussock and mānuka. However, seedling growth was not consistent among species and habitat types. Very few *P. tenuifolium* seedlings died and most survived and grew – mean growth ratios in both caged and uncaged seedlings planted in tussock were

positive. Of the three species, this appears to be the most robust and suitable for planting into tussock. *Carpodetus serratus* and *Melicytus lanceolatus* seedlings had lower survival, and a higher percentage of sickly plants (growth ratio of < 0.3). The increasing importance of environmental gradients found for planted seedlings compared to seeds is consistent with a review of sowing experiments which found abiotic filters can apply more strongly to seedling survival and growth than to seed germination (Turnbull, Crawley & Rees 2000).

Facilitation and protection from herbivory

The third research question I addressed was whether the effect of caging was consistent in both habitat types. I found the protective effect of both nurse species (if any) is not sufficient to protect seeds and young seedlings: in tussock, only 5% of uncaged seeds germinated and survived as seedlings at the one year mark, compared to 22% of caged seeds. I did not find caging to be as important for seedling growth; it appears that seeds and small seedlings are more vulnerable to seed predation and herbivory. This effect is consistent with the differential effect of possums on seeds and seedlings (Jane & Pracy 1974b; Allen, Payton & Knowlton 1984; Stewart & Burrows 1989). It is likely that the mesh used in the seedling experiment exacerbated the shading in the mānuka areas and ameliorated the lack of shade in tussock areas. Therefore I consider that the 'caging effect' has the potential to be conservative in mānuka habitat types and less conservative in tussock habitat types. To summarise, caging had a consistently positive effect on seed germination and establishment in both habitat types, and had an inconsistent effect on planted seedling survival and growth, limited to one species (*M. lanceolatus*).

Environmental variables or habitat type?

The final research question was whether seed establishment and seedling growth was more correlated with environmental variables or the habitat type. Seed germination and establishment in *P. crassifolius* was more strongly influenced by caging and habitat types than any of the variables measured. Because habitat types often had similar values of their environmental parameters (although the range of environmental types within tussock habitat

types was larger) I consider this difference is likely driven by canopy type, which has been found to have significant effects on seedling germination and growth (see Chapter 2).

All three planted species were negatively affected by higher water tables (depth to groundwater). In wetter areas *M. lanceolatus* and *P. tenuifolium* grew less; in the wettest plots no healthy *C. serratus* remained, suggesting there are abiotic thresholds to successful seedling establishment in the wetland and supporting the hypothesis tussock that will persist (or at least remain uninvaded by forest species in wetter areas). Seedlings in tussock areas showed sign of radiation stress (Figure 5.11). As other environmental variables I measured did not come out as important in the model subsetting, I consider it is most likely the remaining difference in seedling growth due to habitat type is the lack of shade provided by *C. rubra*.

Implications for conservation management

Limits to restoration (or 'thresholds') have been recognised in relation to abiotic variables, including changes in hydrology (Hobbs & Norton 2004). Changes in hydrology in wetlands following forest clearance have been noted by Roy, Ruel and Plamondon (2000) and McGlone (2009). Overall, tussock performed more poorly as a nurse species than mānuka for native forest plants and seeds, but appears to be capable of supporting planted seedlings, particularly in drier areas. Later successional, native forest species have previously been documented as invading tussock only after mānuka has done so (e.g. Rogers and Leathwick (1994)); mānuka invasion of tussock was observed in site selection for this experiment. Restoration ecology can require value-laden judgements (Choi 2007), and a question that cannot be addressed through experimental work is whether, merely because it is possible to establish later-successional plants in tussock, this should be done. *Chionochloa rubra* has been 'virtually eliminated' off the Southland plains (Mark & McLennan, 2005, p 261) due to land use intensification. In drier areas, the 'end point' in a Clementsian (Clements 1916) view of regeneration is later successional forest, active restoration efforts in tussock areas would be creating a novel successional pathway. Overall, I

consider the risks of gorse invasions (Chapter 2) and fire (Chapter 6), the inevitability of mānuka invasion in the drier areas, and the benefits of faster forest regeneration for lowering the likelihood of large fires in the wetland mean using *C. rubra* as an alternative location for regeneration plantings should be seriously considered.

Experimental limitations

Seed germination was poorer in tussock, but that was based on only responses of a single species because old seed meant other species provided too little information. I consider that the effect of nurse species and environmental gradients on native forest seed germination and establishment would benefit from having more research with more viable seed of more species.

5.5 Conclusions

This is the first time a native grassland species has been considered and tested as a nurse species for native forest in New Zealand. I consider it deserves further attention. There is a relatively short time window in which ephemeral tussock communities persist prior to invasion (Rogers & Leathwick 1994); there is a relatively long time period for forest species to succeed mānuka once it establishes (Williams & Karl 2002). Tussock did not perform as well as mānuka as a nurse species; but more than half of the caged seedlings of all species survived more than one year. Depth to groundwater was a better correlate of seedling success than habitat type; both nurse species were found in the full range of groundwater depths, and planted seedlings did poorly when the water table was high in both mānuka and tussock. Additional negative effects of tussock were most likely because tussock, while relatively tall for a grassland species, provides less shade for the seedlings. I recommend that in areas where there is a need for fast forest restoration and where surrounding mānuka is young, establishing seedlings in tussock is likely to be worthwhile. So long as particularly wet areas are avoided (depth to groundwater at least 20 cm, on average), truncation of the natural tussock niche will be avoided and seedling success maximised. I recommend providing some form of shade protection combined with protection from herbivory, where practicable. Where this is

provided, I consider it will be possible to skip a successional stage and jump start regeneration by creating small pockets of seed sources within the tussock, ephemeral tussock and mānuka matrix.

Appendix 5.1: Sown *Pseudopanax crassifolius* establishment

Table 5.2: Sown seed germination and survival rates for *Pseudopanax crassifolius*, averaged across all locations.

Habitat type	Caging treatment	Date measured	Proportion surviving	SE
Mānuka	Caged	1/03/14	0.35	0.077
Mānuka	Caged	8/05/14	0.36	0.078
Mānuka	Caged	10/12/14	0.35	0.091
Mānuka	Uncaged	1/03/14	0.30	0.067
Mānuka	Uncaged	8/05/14	0.23	0.076
Mānuka	Uncaged	10/12/14	0.19	0.071
Tussock	Caged	1/03/14	0.15	0.062
Tussock	Caged	8/05/14	0.17	0.068
Tussock	Caged	10/12/14	0.22	0.077
Tussock	Uncaged	1/03/14	0.13	0.063
Tussock	Uncaged	8/05/14	0.14	0.064
Tussock	Uncaged	10/12/14	0.05	0.045

Appendix 5.2: Effect of abiotic variables on *Pseudopanax crassifolius* establishment model selection table

Table 1: Model selection table. The following variables (interactions denoted by the form variable a : variable b) are not shown as they appeared in none of the AICc < 4 models: habitat : mean depth to groundwater; habitat : CV groundwater; habitat : total P. df represents the number of used degrees of freedom. Coefficients are presented for continuous variables, a + symbol for factors indicates their inclusion in the model.

(Intercept)	Caging	CN ratio	CV GW	Habitat type	Mean GW	Total P	Caging:habitat	df	logLik	AICc	delta	weight
-1.37	+							4	-70.70	151.51	0.00	0.23
-0.53	+			+				5	-69.12	151.57	0.06	0.23
-4.20	+	0.108						5	-69.95	153.24	1.73	0.10
-0.12	+				-0.037			5	-70.25	153.83	2.32	0.07
-2.11	+		0.014					5	-70.36	154.06	2.55	0.06
-0.72	+			+			+	6	-68.69	154.32	2.81	0.06
-2.53	+	0.073		+				6	-68.72	154.37	2.87	0.06
0.43	+			+	-0.029			6	-68.75	154.43	2.93	0.05
0.61	+			+		-0.002		6	-68.83	154.60	3.09	0.05
-1.00	+					-0.001		5	-70.67	154.68	3.17	0.05
-1.07	+		0.009	+				6	-68.92	154.79	3.28	0.04

Appendix 5.3: Effect of abiotic variables on *Pseudopanax crassifolius* establishment model averaged coefficients

Table 5.2: Model averaged coefficients for the global model for seedling survival for *P. crassifolius* seedlings. Model formula was in the form of glmer(formula = cbind(count, 40 - count) ~ caging * habitat + mean_gw + mean_gw:habitat + CN.ratio + total.P:habitat + cv_gw + cv_gw:habitat + total.P + (1 | location/caging), data = tseeds_psecra, family = binomial, na.action = na.fail), including only those models for which the delta AICc was < 4. Caging is the only significant effect (p = 0.005).

	Estimate	Std Error	Adjusted SE	z value	p value
Intercept	-1.22	1.80	1.87	0.65	0.514
Caging - uncaged	-1.78	0.60	0.64	2.78	0.005
Habitat - tussock	-0.78	1.05	1.08	0.73	0.466
CN ratio	0.01	0.05	0.05	0.29	0.772
Mean depth to groundwater	0.00	0.02	0.02	0.24	0.811
CV depth to groundwater	0.00	0.01	0.01	0.19	0.848
Caging - uncaged : habitat - tussock	-0.06	0.35	0.37	0.16	0.873
Total P	0.00	0.00	0.00	0.13	0.897

Appendix 5.4: Planting experiment – survival data

Table 5.3: Sown seedling survival 13 months post-sowing (December 2014)

Species	Habitat	Caging	Total sown	Total surviving	Mean proportion surviving	SE
P. tenuifolium	Mānuka	Caged	30	30	1.00	0.00
P. tenuifolium	Mānuka	Uncaged	30	28	0.93	0.07
P. tenuifolium	Tussock	Caged	30	28	0.93	0.07
P. tenuifolium	Tussock	Uncaged	30	30	1.00	0.00
C. serratus	Mānuka	Caged	30	21	0.70	0.11
C. serratus	Mānuka	Uncaged	30	20	0.67	0.15
C. serratus	Tussock	Caged	30	17	0.57	0.17
C. serratus	Tussock	Uncaged	30	15	0.50	0.17
M. lanceolatus	Mānuka	Caged	24	19	0.79	0.16
M. lanceolatus	Mānuka	Uncaged	24	17	0.71	0.19
M. lanceolatus	Tussock	Caged	24	19	0.79	0.16
M. lanceolatus	Tussock	Uncaged	24	9	0.38	0.15

Appendix 5.5: Effect of abiotic variables on planting experiment heights – variable importance

Table 5.4: The most important environmental variables correlating with seedling height gain. Relative variable importance for all variables included within the delta AICc < 4 subset of models.

Variable	Relative importance
Species	1.000
GW	0.923
Habitat	0.796
Species : GW	0.554
GW : habitat	0.551
Species : habitat	0.255
Species : GW : habitat	0.255

Appendix 5.6: Effect of abiotic variables on planting experiment heights – model selection table

Table 5.5: Model selection table for seedling heights change analysis. GW = depth to groundwater, included as a polynomial term. Only those variables included within the subset of models for which delta AICc are included. The model was in the form of height_ratio ~ species + habitat + species:habitat + caged + species:caged + species:habitat:caged + poly(mean_gw, 2) + poly(mean_gw, 2):habitat + poly(mean_gw, 2):habitat:species + CN.ratio + species:cv_gw + cv_gw+ habitat:cv_gw + species:poly(mean_gw, 2) + (0 + species|location/caged) + (1|location/caged), specified with a Gaussian distribution. CN.ratio = carbon-nitrogen ratio; poly(mean_gw, 2) = 2nd order polynomial of depth to groundwater (expressed in centimetres); cv_gw = coefficient of variation for the depth to groundwater at each site. df represents the number of used degrees of freedom. Coefficients are presented for continuous variables, a + symbol for factors (or factor : continuous interactions) indicates their inclusion in the model. GW included as a + because of the polynomial term (see Appendix 5.7).

(Int)	Habitat	GW	Species	Habitat : GW	Habitat : species	GW : species	Habitat : GW : species	df	logLik	AICc	delta	weight
1.115	+	+	+	+	+	+	+	33	57.326	-38	0	0.255
1.129	+	+	+	+				23	44.107	-37.2	0.77	0.173
1.138	+	+	+					21	41.493	-36.8	1.14	0.144
1.14	+	+	+	+		+		27	48.751	-36.5	1.46	0.123
1.153	+	+	+			+		25	46.043	-36.1	1.84	0.101
1.012			+					18	37.309	-35.6	2.39	0.077
1.04		+	+			+		24	44.507	-35.5	2.43	0.076
1.005		+	+					20	39.26	-34.8	3.21	0.051

Appendix 5.7: Effect of abiotic variables on planting experiment heights – model averaged coefficients

Table 5.6: Model summary for model averaged coefficient model for plant height ratios change analysis. Predictions based on this model are presented in Figure 5.9.

Variable	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)
(Intercept)	1.42	0.09	0.09	16.17	< 2e-16
habitatTussock	-0.23	0.14	0.14	1.65	0.100
poly(mean_gw, 2)1	0.99	0.79	0.80	1.24	0.215
poly(mean_gw, 2)2	-0.82	0.77	0.77	1.07	0.287
speciesC. serratus	-0.31	0.06	0.06	4.85	0.000
speciesM. lanceolatus	-0.29	0.09	0.10	3.04	0.002
habitatTussock:poly(mean_gw, 2)1	0.62	1.09	1.09	0.56	0.574
habitatTussock:poly(mean_gw, 2)2	-0.03	1.05	1.06	0.03	0.979
habitatTussock:speciesC. serratus	0.06	0.12	0.12	0.48	0.634
habitatTussock:speciesM. lanceolatus	-0.04	0.11	0.11	0.34	0.731
poly(mean_gw, 2)1:speciesC. serratus	-0.58	0.99	0.99	0.59	0.556
poly(mean_gw, 2)2:speciesC. serratus	0.86	1.17	1.17	0.74	0.461
poly(mean_gw, 2)1:speciesM. lanceolatus	0.45	1.20	1.21	0.37	0.710
poly(mean_gw, 2)2:speciesM. lanceolatus	0.22	1.07	1.07	0.20	0.838
habitatTussock:poly(mean_gw, 2)1:speciesC. serratus	-0.55	1.69	1.69	0.33	0.744
habitatTussock:poly(mean_gw, 2)2:speciesC. serratus	0.53	1.76	1.76	0.30	0.765
habitatTussock:poly(mean_gw, 2)1:speciesM. lanceolatus	-0.51	1.63	1.64	0.31	0.757
habitatTussock:poly(mean_gw, 2)2:speciesM. lanceolatus	-0.71	1.96	1.97	0.36	0.718

Appendix 5.8: Planting experiment heights – plant weights analysis

Table 5.7: Mean net dry weight (g) of seedlings at end of experiment and standard error.

Species	Habitat	Caged	Mean weight (g)	SE
P. tenuifolium	Mānuka	Caged	3.99	0.49
P. tenuifolium	Mānuka	Uncaged	4.43	0.33
P. tenuifolium	Tussock	Caged	5.79	0.36
P. tenuifolium	Tussock	Uncaged	4.95	0.51
C. serratus	Mānuka	Caged	6.99	0.42
C. serratus	Mānuka	Uncaged	6.93	0.52
C. serratus	Tussock	Caged	7.61	0.31
C. serratus	Tussock	Uncaged	5.84	0.36
M. lanceolatus	Mānuka	Caged	3.96	0.27
M. lanceolatus	Mānuka	Uncaged	3.76	0.30
M. lanceolatus	Tussock	Caged	3.80	0.29
M. lanceolatus	Tussock	Uncaged	3.24	0.22

Table 5.8: Generalised linear mixed effects model output of plant weights. All plants were included. Model included random slope term for species with correlated intercept of caging treatment nested within sites. Species codes are as follows: CARSER – *C. serratus*; MELLAN – *M. lanceolatus*; PITTEN – *P. tenuifolium.*

	Value	Std.Error	DF	t-value	p-value
(Intercept)	3.99	0.87	300	4.59	0.000
CARSER	*3.00*	*0.76*	*300*	*3.93*	*0.000*
MELLAN	-0.02	0.81	300	-0.03	0.976
PITTEN : tussock	1.81	1.23	300	1.47	0.142
CARSER: tussock	0.62	0.78	300	0.80	0.426
MELLAN : tussock	-0.16	0.64	300	-0.25	0.801
PITTEN: uncaged	0.44	1.09	300	0.41	0.685
CASER: uncaged	-0.06	0.61	300	-0.10	0.917
MELLAN: uncaged	-0.24	0.50	300	-0.48	0.633
PITTEN : tussock : uncaged	-1.29	1.54	300	-0.83	0.405
CARSER : tussock : uncaged	*-1.71*	*0.86*	*300*	*-2.00*	*0.047*
MELLAN : tussock : uncaged	-0.32	0.71	300	-0.45	0.653

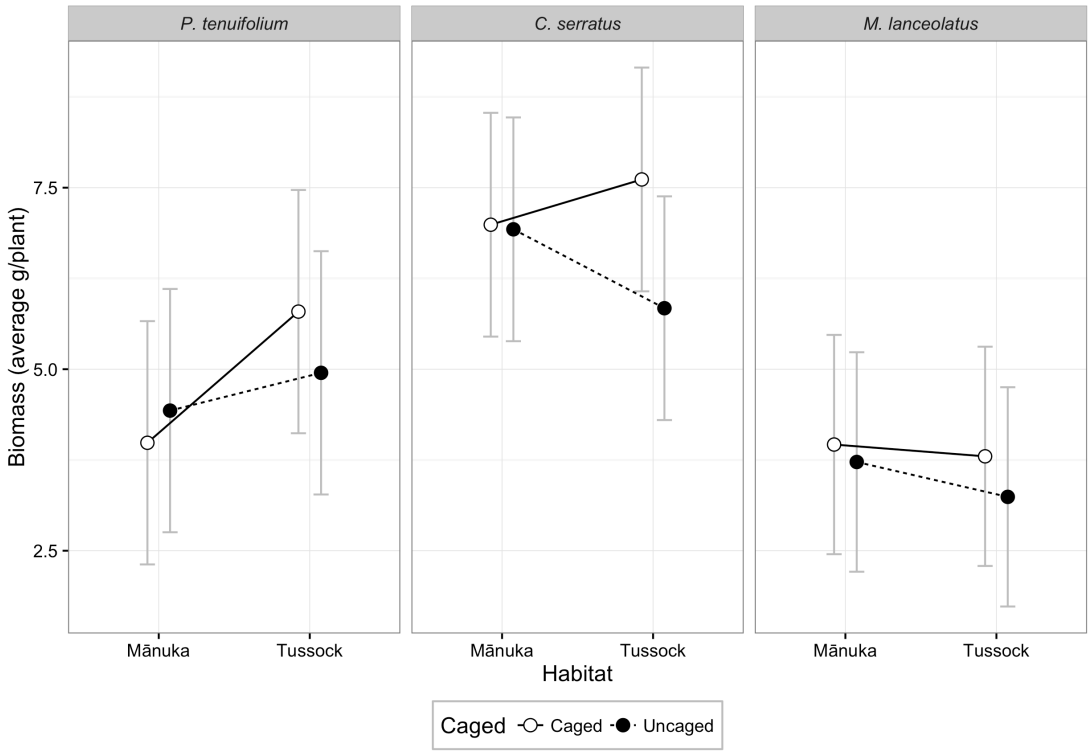


Figure 5.12: Predicted mean weights (g) and confidence intervals for plants 13 months post-planting. *C. serratus* was significantly heavier than *P. tenuifolium*, and the effect of caging was significantly different for *C. serratus* only (see Table 5.8).

Chapter Six: Spatially explicit models of regeneration in Awarua wetland

6.1 Introduction

Landscapes (a spatially heterogeneous area of land: Turner, Gardner and O'Neill (2001)), and landscape ecology (the study of relationships between ecological flows and processes and spatial patterns of landscapes through time (Forman 1983)) are important considerations in ecological restoration when ecosystems are fragmented (SER [Society for Ecological Restoration International Science & Policy Working Group] 2004). Landscape simulation models have a long pedigree of use in exploring forest dynamics (Baker & Mladenoff 1999; Mladenoff & Baker 1999; Bachelet *et al.* 2000) and management options (e.g., LANDIS – see Scheller *et al.* (2007)), and are amenable to simulating fragmented landscapes.

Models can be generally classed as 'predictive' or 'exploratory' (Perry & Millington 2008). Predictive models are, as the name suggests, focused on predicting the dynamics of a system, and can take the form of regression modelling and species distribution models, both of which were undertaken in Chapter 2. Exploratory (or heuristic) modelling is more focused on understanding the dynamics of the system, and can be used to assist with conservation management (Perry & Millington 2008). In New Zealand, spatially explicit models have been used to explore the causes and patterns of fire that led to wide-spread deforestation following Maori settlement (Perry *et al.* 2012), to simulate gap dynamics and responses to disturbance with a modified North American ('LINKNZ') model (Hall & Hollinger 2000), and to model forest depletion in eastern Southland and Otago, using the LINKNZ model (Hall & McGlone 2001), which has also been used in a landscape planning setting (Meurk & Hall 2006). Most recently, spatial models have been used to detect synergistic

effects on succession between herbivory and seed predation, invasive plants and fire (Perry *et al.* 2015).

Simulation modelling was undertaken to better understand landscape scale ecological processes where a number were observed to influence patterns of community assembly. These included dispersal limitation shown through quantitative experiments (Chapter 2); an observed lack of seed sources for many areas in the wetland (refer Figure 2.1, Chapter 2, and Figure 6.11, below); the negative effects of seed predation and seedling herbivory on regeneration (Chapters 2 and 5); and the recurrent fires within the wetland that could combine to affect forest regeneration.

Fire activity in New Zealand increased after Maori arrival, substantially reducing forest cover (McWethy *et al.* 2010; Perry *et al.* 2012), and then increased again after European settlement (Ewers *et al.* 2006). Fire can lead to alternative stable states in New Zealand because it promotes early stage vegetation dominated by native fire-adapted species (e.g. *Leptospermum scoparium* - Esler and Astridge (1974), Enright (1989)) or exotic pyrophyllic taxa (McQueen & Forester 2000; Perry *et al.* 2015). A high proportion of early successional vegetation leads to a landscape of 'peak flammability' and increased susceptibility to fire ignition and spread; this state can last for decades (Kitzberger *et al.* 2012), whereas later successional species can reduce the overall flammability of the area (Odion, Moritz & DellaSala 2010; Perry *et al.* 2012) (Figure 6.1).

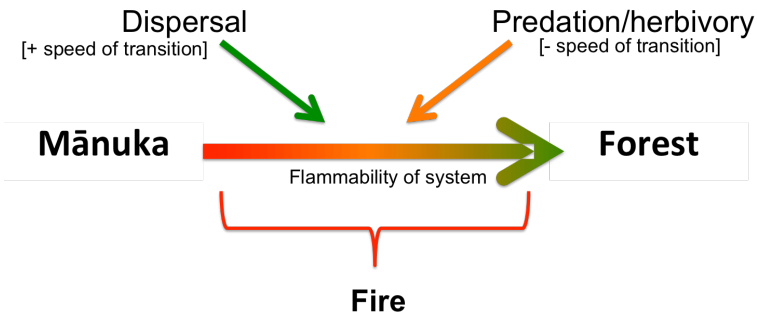


Figure 6.1: Conceptual overview of succession as affected by fire, vegetation composition, dispersal and herbivory and predation. Fire resets the system at any time to early successional grassland and shrubs.

The dominance of mānuka in Awarua wetland in terrestrial areas is considered to have been induced by anthropogenic disturbance – clearing, drainage, and fire (Johnson 2001). The increase in early-successional species and mānuka in the pollen record correlates with increased charcoal following Maori and European settlement periods (Wilmshurst J, 2015, pers. comm.). Contemporary fires kill mid- and late-successional vegetation, leaving burnt areas to regenerate with grass and tussock species, mānuka, and invasive shrub species (Johnson 2001).

Seed limitation, seed predation, and seedling herbivory can all be expected to extend the duration of peak flammability by slowing the rate of natural forest regeneration (Wunderle Jr 1997; Wilson *et al.* 2003; de Souza Gomes Guarino & Scariot 2014). I therefore sought to test the relative importance of these parameters to (modelled) forest regeneration by answering the following research questions:

1. What parameters is the model most sensitive to, in terms of whether landscapes reached 75% forest at the end of 500 years?
2. What parameters is the model most sensitive to, in terms of the speed at which landscapes reach 75% forest?
3. How important is the current landscape spatial configuration in determining modelled trajectories?

6.2 Methods

I designed a state-and-transition model (Bestelmeyer *et al.* 2010) representing the wider Awarua catchment (55,842 ha) to model forest succession across a range of parameters (Figure 6.2). In particular, I sought to quantify the importance of dispersal, land use, predation/herbivory and anthropic fires to forest regeneration.

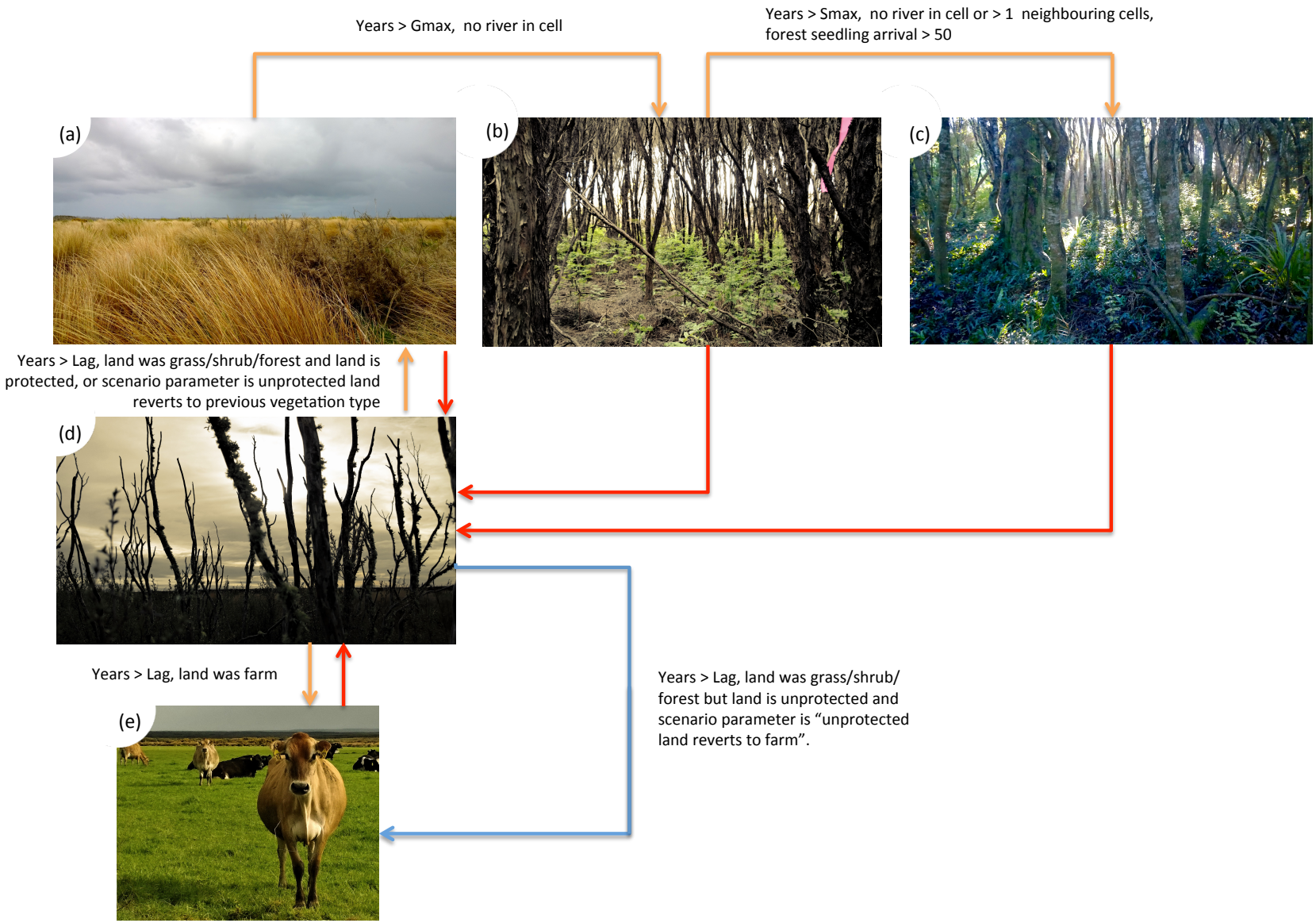


Figure 6.2: Schematic view of succession as represented in the spatial state and transition model. Red lines indicate succession after fire. Yellow lines indicate succession after fire to farmland or to grassland, followed by shrub and forest. Blue line indicates an alternate transition modelled where unprotected grass, shrub or forest on private land would be converted to farmland if burnt. (a) grassland (*Chionochloa rubra* and *Ulex europaeus*). Gmax is a parameter in the model specifying the minimum succession time between grass and shrub. (b) shrub, in this case mānuka (*Leptospermum scoparium*) with a water fern (*Histiopteris incisa*) understorey. Smax is the minimum succession time between shrub and forest. (c) Forest, dominated by kāmahi (*Weinmannia racemosa*). (d) Burnt mānuka stems. Lag is a parameter in the model specifying the minimum period before burnt land can be recolonised by grass (native, or in farmland). (e) Farmland adjacent to the wetland. All photos taken in the wetland catchment by Olivia Burge.

Model design

This section provides a non-technical overview of the model design; for specifics, see Appendix 6.1, which provides a description of the model following the recommendations in Grimm *et al.* (2010).

The model was created in NetLogo (Wilensky 1999) and implemented in R using package RNetLogo (Thiele, Kurth & Grimm 2012). NetLogo allows the implementation of multi-agent, spatially explicit models. I simulated an area that encompassed all but the northernmost portion of the Awarua catchment (Figure 6.3).

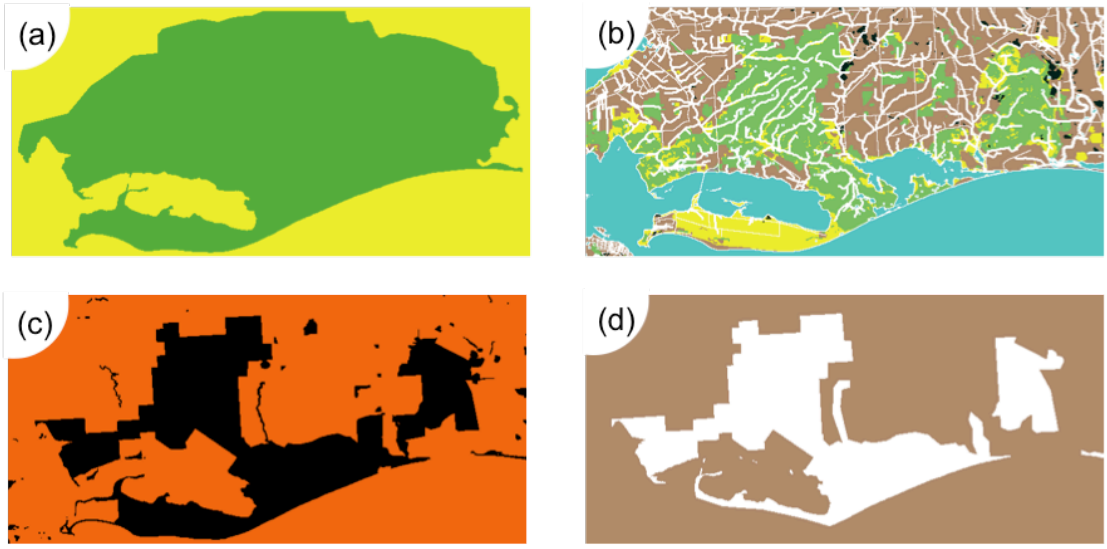


Figure 6.3: A spatial overview of GIS layers underlying the Netlogo model, the extent of which is 34 km x 16 km (55,700 ha): (a) The Ramsar catchment as implemented in Netlogo. The northern-most portion (refer Figure 1.2, Chapter 1, for catchment overview) is excluded from the model. Green indicates the area within the catchment. (b) The starting vegetation values (light green = shrub, yellow = grass, dark green = forest, brown = farmland) in the model overlain with the 'terminal shrub' areas in white, in which forest could not grow. These setback areas include roads, rivers and setbacks from them (see Appendix 6.1 for details). (c) Protected areas (conservation estate or private land under conservation covenants) are shown in black. These areas are not consistent with the Ramsar boundary (although similar). (d) The listed Ramsar area, excluding coastal areas but including Waituna lagoon, is shown in white.

The landscape was made up of square 'patches' (grid cells), each representing an area of 50 x 50 m. I used a shapefile of the New Zealand coastline from Land Information New Zealand (based on the 1:50,000 NZTopo database) for the coastline of New Zealand. I used a shapefile from Land Information New Zealand

(based on the 1:50,000 NZTopo database) for the rivers in the catchment that I overlaid on the landscape. I created a vegetation raster layer of the same resolution (50 x 50 m) by blending two datasets: the more detailed existing vegetation mapping used in Chapter 2 (Anon. 2010), and the Land Cover Database (LCDB, version 4.1, 2012 vegetation layers) for New Zealand, as the existing vegetation mapping did not cover the entire model landscape. I used the existing vegetation mapping for areas in which it existed, and LCDB only for areas that existing vegetation mapping did not cover. Areas mapped as later successional forest (e.g. LCDB 2012 areas mapped as "broadleaved indigenous hardwoods" or "indigenous forest") were categorised as forest, while shrub species (e.g., mānuka, grey scrub in the existing vegetation mapping) and grass species (e.g. red tussock and flaxland in the existing mapping and LCDB 2012 respectively) were categorised correspondingly. While the majority of the surrounding catchment is in intensive agriculture (refer Figure 1.3, Chapter 1), areas not covered in vegetation were classed as either 'impermeable' or 'farmland'. Impermeable land types were limited to areas mapped as surface mines, sand and gravel, and gravel and rock (all LCDB categories). Farmland was everything else, primarily composed of high-productivity exotic grassland and low producing grassland, but also including exotic forestry and small open space (non-conservation estate) areas.

Each vegetation and land use type (water, farmland, grass, shrub, forest) had a flammability state, from 0 (water) to grass (1), which affected the likelihood of whether they would burn when struck by lightning, or by fire spreading from neighbouring cells. These values were designed to implement the relative successional flammability values discussed in the introduction into the model. Forest was set to 0.2 and shrub to 0.5. Patches with rivers running through them had their flammability modified downwards by 10% (i.e., river patches were 90% as flammable as non-river patches of a corresponding flammability). The flammability state was multiplied by the landscape flammability value (which varied between models) and affected the likelihood of a patch burning.

I parameterised natural fire (lightning) using rates derived from historical data (Etherington T, 2015, pers. comm.). I simulated farm fires by varying the number of annual 'large', out-of-control farm fires (the fires of interest) between models. The number of annual farm fires each year was randomly drawn from a Poisson distribution with a mean held constant for each model, and ranged from 0 – 4. The size of fires when they ignited at the wetland edge also varied. All fires spread as a front using a percolation process (O'Sullivan & Perry 2013), with the likelihood of spread into a cell depending on that cell's flammability and an element of random change (Figure 6.4).

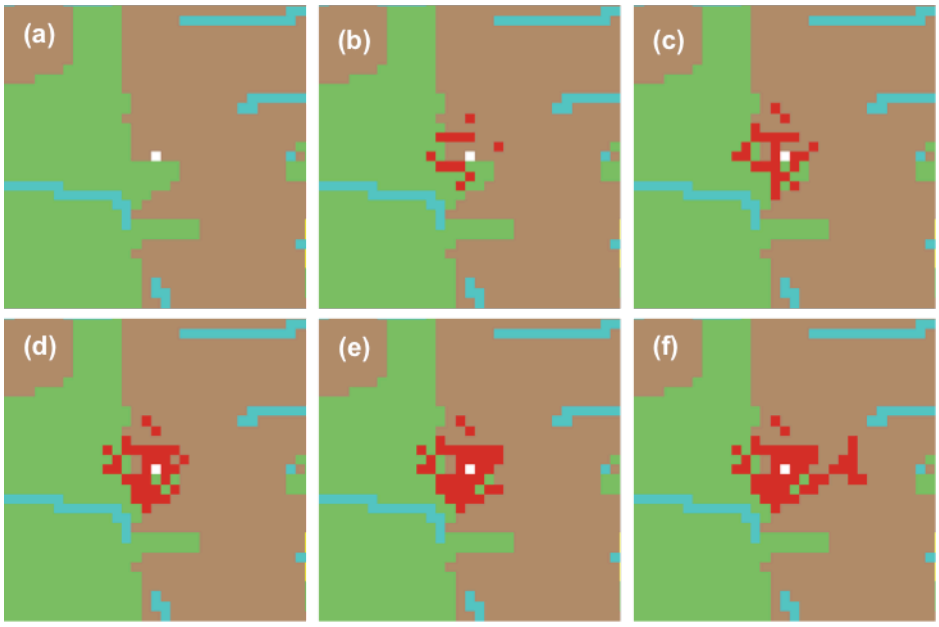


Figure 6.4: Example of farm fire ignition and spread in the Awarua NetLogo model. (a) White patch indicates 'ignition' patch for all timesteps. (b) Starting farm fire size shown in red around ignition patch (in this case, 8 cells) which ignite in a four-cell radius. (c) – (e) each show steps in the farm fire front. Lightning fire spreads in the same way as these cells. (f) Final extent of fire shown in red, with initial ignition point in white. (a) – (f) happen in one time-step.

Vegetation could transition between vegetation types each time-step (Figure 6.2), which was equivalent to a year in real time. After a fire, burnt areas could transition to grass following a short lag; grass could transition to shrub if it did not have a river running through the patch and a time threshold (varied between models) had passed. Shrub could transition to forest provided it had reached a sufficient density of forest seedlings, it was over the a minimum age threshold

(the threshold varied between models) and it was not in a 'terminal shrub' zone. Terminal shrub zones were areas in which a river passed (which could occur if shrub started in a river-containing cell), or next to a patch in which a river passed, or in which a road was located – see Figure 6.3.

Shrub patches could receive forest seeds through seed dispersal, which was modelled phenomenologically. Forest seed dispersal was split into local- and long-distance dispersal (LDD). Local dispersal resulted in forest (and qualifying shrub patches – see Appendix 6.1) patches dispersing seed into adjacent (cells sharing either an edge or diagonal; a Moore neighbourhood) shrub patches. Long-distance dispersal allowed each forest patch dispersing seedlings (discounted by the predation rate) to a patch in a random direction at a distance drawn from an exponential distribution with a mean which varied between model realisations. If shrub was the vegetation type of the receiving patch, the seeds established. Where bird abundance (a variable which varied between models) was less than one, the number of patches undertaking near- and long-distance dispersal was reduced proportionately. For example, if bird abundance was 0.5, 50% of the forest (and qualifying shrub) patches undertook local dispersal, and 50% of the forest patches undertook long-distance dispersal. Patches were chosen at random (subject to qualifying criteria), meaning patches might undertake both local and long-distance dispersal, either, or neither, in each time-step. Qualifying shrub patches undertook local dispersal only, and at a reduced rate (half the seeds dispersed c.f. forest), to simulate the slow process of regeneration percolating from forest fragments. Seeds establish as seedlings over time, subject to reduction by the predation rate. As the number of seedlings in each cell increases, the likelihood of transition (assuming other factors are satisfied) to forest increases.

Seed and seedling predation rate (PR) as a model variable was binary ranging from 0 – 1. It reduced both the number of seeds received post-dispersal by patches ((1 – PR) * seedlings received), and also reduced the number of seedlings surviving over time in each patch through herbivory ((1 – PR)/2 * seedlings received). The predation rate was constant within each model, across

vegetation types. The reduced effect of herbivory on older seedlings is consistent with the results in Chapter 5.

Sensitivity analysis

I varied the predation rate, lags between vegetation transitions, average LDD distance, bird abundance, forest cluster visitation threshold (where birds would not visit very small fragments of forest), mean number of annual farm fires, mean starting farm fire size, and landscape flammability across 2,000 model simulations using a Latin Hypercube Sampling, which allows for uniform sampling of a multivariate parameter space (package LHS: Carnell (2012) in R). Each model ran for 500 years. I tested the importance of variables correlated with successful forest regeneration using boosted regression trees (package DISMO Hijmans *et al.* (2013) in R). Boosted regression trees draw from both machine learning and traditional statistical methods. Unlike traditional regression methods which produce one 'best' model, boosted regression trees combine numerous simple tree models to optimise performance. The 'boosting' element of the name comes from the algorithm that builds and combines the collection of models, while 'regression tree' comes from the regression trees (or 'decision trees') that collectively form the group of models combined by boosting (Elith, Leathwick & Hastie 2008). I used a response variable of whether or not a forest reached or exceeded 75% forest (a Bernoulli response) by 500 years, and for the models that reached or exceeded 75%, the time it took for them to get there (a Gaussian response). Because landscapes could never reach 100% forest (e.g. in ocean areas) the proportion of forest was the proportion of cells in which it was possible to succeed to forest. This included all grass, shrub and forested areas (excluding cells that were prevented from succeeding to forest based on proximity to river cells), but exclude waterbodies (the ocean, the lagoon, and tarns) and farmland.

Landscape configuration analysis

Based on the outcomes of the sensitivity analysis, I decided to investigate how starting landscape configuration and the amount of forest at model initiation,

and the combination of the two, affected the trajectory and rate of forest regeneration.

In addition to the landscape configuration used in the sensitivity analysis, I created two new landscapes. I provide a descriptive overview here, with further details in Appendix 6.1.

Existing landscape configuration ± added forest

I used the landscape configuration described in the sensitivity analysis methods for the existing landscape configuration. I created landscapes with 10% more (additively) forest using two different techniques:

1. the existing landscape + 10% more forest, which replaced existing shrub, in applied nucleation fashion. This involved transforming 20 randomly chosen shrub grid cells to forest, and transforming a varying number of shrub patches around them to forest, until 10% extra was reached.
2. the existing landscape + 10% more forest, which replaced existing shrub, added around the edges of existing forest remnants, until 10% extra forest was reached.

Model parameters

I ran the model across a range of parameters found to be most influential in the sensitivity analysis. As for the sensitivity analysis, model duration was 500 years. Average LDD distance varied between 200 and 800 m in increments of 200 m (e.g., 200, 400, 600 and 800 m). The bird abundance index ranged from 0.2 and 0.8 in increments of 0.2. The predation rate ranged from 0.2 to 0.8 in increments of 0.2. The number of annual farm fires took one of three values – 0.5, 1 and 1.5. The experimental design was fully orthogonal, leading to 192 parameter combinations. Each set of parameter combinations was run for each starting configuration (n = 3) leading to 576 model simulations in a series. Each series was run five times, for a total of 2880 models. These simulations were relatively computationally prohibitive even on a supercomputer (I used the New Zealand eScience Infrastructure high performance computing facilities at the

University of Auckland), preventing me from running further replicates or considering other landscape configurations.

Statistical analysis

I hypothesised that that increasing forest would increase the end-of-model proportion of forest in the landscape. I also sought to test for a difference in restoration methods (nucleation vs edge planting). I used a generalised linear mixed effects model (GLMM) in R version 3.2.2 (R Core Team 2015) because the initial generalised linear model was overdispersed (residual deviance = 2,912,142; residual df = 2,874). The GLMM was implemented using package LME4 (Bates *et al.* 2014), with a binomial response in the form of the number of patches in forest as a proportion of the total potential (see transition rules above) forest patches at model initiation, which was a constant 61,504. The fixed effects were starting configuration (a factor) and average LDD distance, a numeric variable, and the interaction between the two. I included a random intercept for each model nested within series.

6.3 Results

In the sensitivity analysis, I tested the probability of landscapes reaching 75% forest in areas in which it was possible to do so. Of the 2,000 models in the sensitivity analysis, 628 reached 75% forest, and took an average of 317 ± 4 years (mean ± standard error).

I tested which variables were most correlated with the probability of a landscape reaching 75% forest in 500 years, and the length of time it took to achieve it. I tested these relationships using boosted regression trees, using formulae developed by Friedman (2001) to estimate the relative importance of each of the predictor variables. Variable importance is based on how many times a variable is selected in each tree, and the improvement it makes to the tree's explanatory power, averaged over all trees. Relative influence is scaled to sum to 100, with high values awarded to variables with stronger influence.

What were the most important variables predicting whether landscapes reached 75% forest at the end of 500 years?

I tested variable importance using a boosted regression tree with a binary (0/1) response (Figure 6.5). The two most important variables correlated with landscapes reaching 75% forest were associated with seed dispersal. The most important was the average long distance dispersal (LDD) distance (variable importance = 31.80), followed by bird abundance (variable importance = 20.10). This was followed by the seed predation and seedling herbivory rate (variable importance = 13.85) and the number of annual farm fires (variable importance = 13.05).

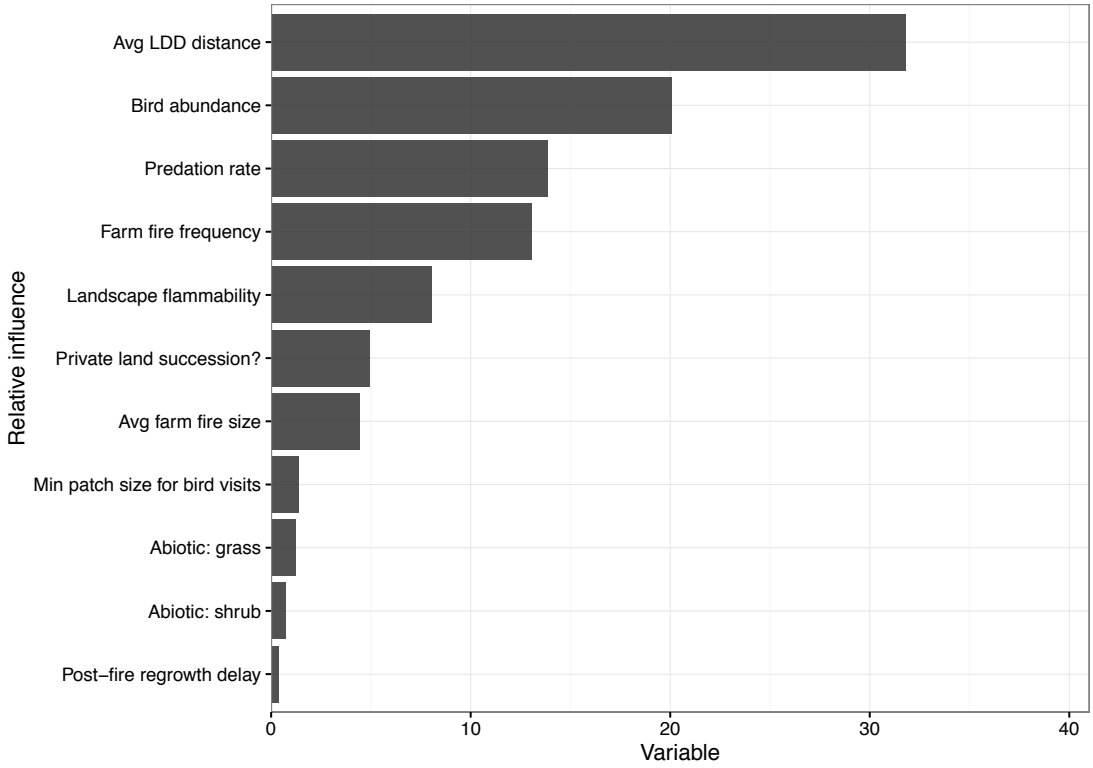


Figure 6.5: Boosted regression trees sensitivity to variables affecting model outcome of 75% forest cover at the end of 500 years. The mean long distance dispersal distance is the most important determinant of whether landscapes attain 75% forest (results of boosted regression tree). Relative important is based on how often variables among all regression trees (in this case, 3800 iterations).

Average LDD distance and bird abundance were positively correlated with an increasing chance of reaching 75% forest (Figure 6.6). There was a sharp rate of increase in the likelihood of reaching 75% forest as average LDD moved from

200 m to > 500 m provided that bird abundance was ≥ 0.4. Bird abundance is an index of 0 – 1, and represents the number of grid cells (50 x 50 m areas) that are inhabited by birds in any one year. At low levels of bird abundance, landscapes were unlikely to reach 75% forest even where the average LDD was high. There was little difference between bird abundances of 0.7 and 1 (the lines overlap on Figure 6.6), meaning there was no noticeable gain in increasing bird abundance from an average of 70% of patches in a landscape being inhabited by birds to the landscape being saturated with birds. The likelihood of a landscape having > 75% forest was relatively insensitive to the effect of seed predation and herbivory, except where it was high (≥ 90%), at which point only landscapes with high bird abundance and moderate-high average LDD distance were likely to reach 75% forest coverage. Predation also synergistically interacted with bird abundance; decreases in bird abundance were exacerbated by increasing levels of seed predation and seedling herbivory.

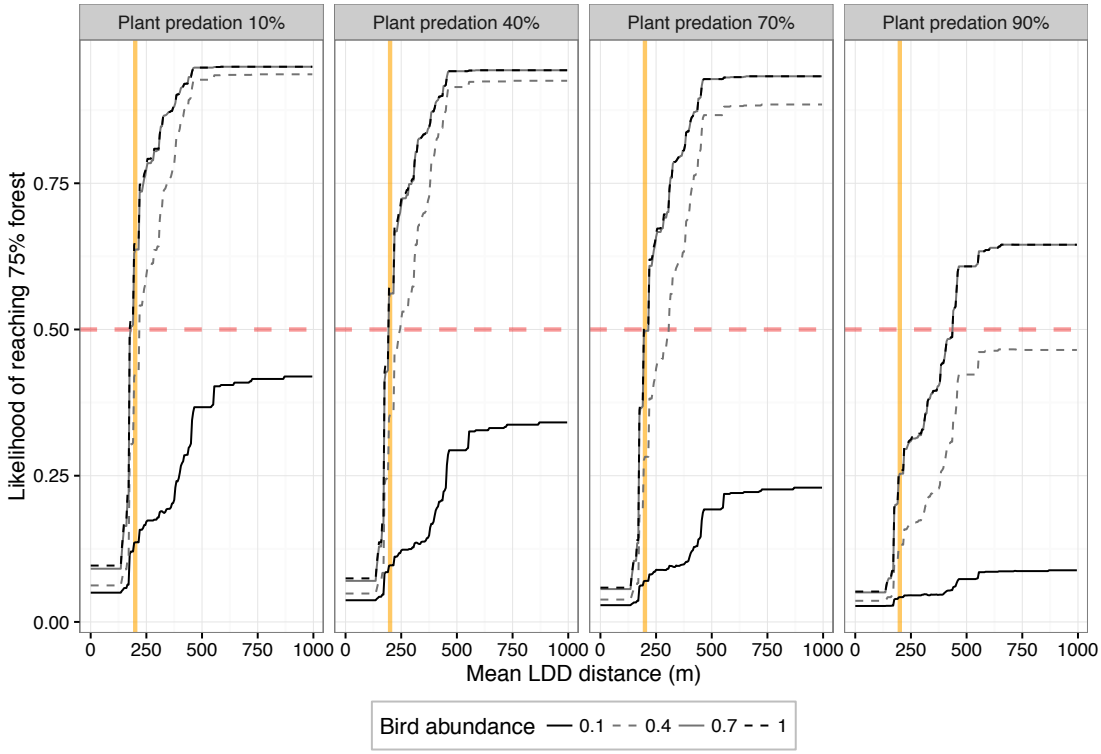


Figure 6.6: Predicted probability of landscapes reaching 75% forest based on boosted regression trees (n = 500 trees for prediction), all other variables held to their mean except post-fire private land use of non-farmland (a factor), which is set to reverting to grass after fire rather than farmland. Mean long distance dispersal needs to be > 200 m (indicated by yellow line) for landscapes to be

more likely than not to reach 75% (50% likelihood of reaching 75% forest indicated by red dashed line). Reduced relative bird abundance interacts with the mean long distance dispersal distance and the predation rate to reduce the likelihood of landscapes reaching 75%.

In the Ramsar catchment, there were 1519 grid cells of forest, of which 792 (52%) were protected. Land-use rules prevent the clearance of indigenous vegetation over 25 years old under operative Southland District Plan (the relevant provisions of the proposed District Plan are subject to appeal and non operative). Following fire, unprotected areas of native vegetation may revert to farmland (grey lines in Figure 6.7) or be allowed to succeed to grassland, to shrub and then to forest. The negative effect of reverting to farmland (grey line) increases as the rate of farm fire increases. At current annual farm fire rates (orange shaded area), the effect of land-use rules is more important where fires are large and where average LDD distances are moderate. Even then, the effects are swamped by changes in average LDD distance. Probabilities are relatively high – above 50% (red line) because variables such as bird abundance index and predation are held to their means (0.5 and 50%, respectively). Predictions were derived from boosted regression tree model (n = 500 trees for prediction), all other variables held to their mean.

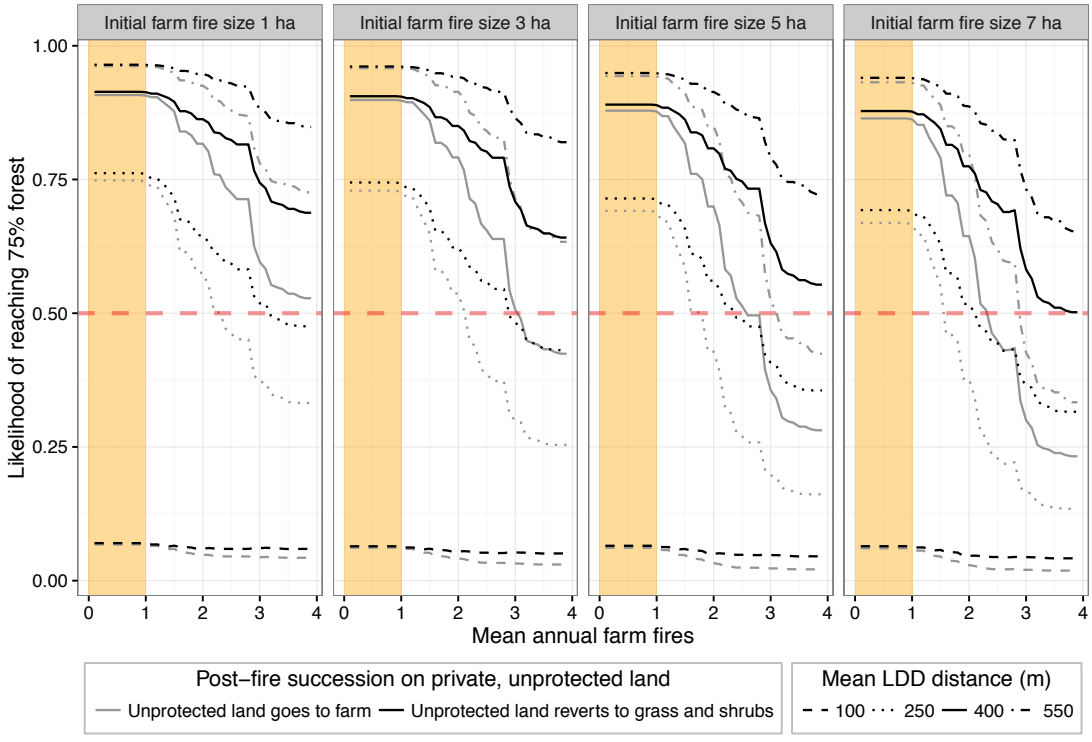


Figure 6.7: Predicted likelihood of landscapes reaching 75% forest based on boosted regression trees (n = 500 trees for prediction), all other variables held to their mean. Likelihoods are relatively

high – above 50% (red line) because variables such as bird abundance index and predation are held to their means (0.5 and 50%, respectively). Red dashed line indicates the 50% likelihood cut off. Land use rules prevent the clearance of native vegetation over 25 years old (operative Southland District Plan). Following fire, these areas may revert to farmland (grey lines) or be allowed to succeed to grassland, to shrub and then to forest. The negative effect of reverting to farmland (grey line) increases as the rate of farm fire increases. The current annual farm fire rates are shown in the orange shaded area.

The frequency of annual farm fires was the fourth most important variable correlated with the likelihood of landscapes reaching 75% forest (variable importance = 13.05). The number of farm fires each year, within each model, was determined by drawing a random integer from a Poisson distribution with a mean of the annual farm fires. For example, if a landscape has an annual farm fire rate of 0.5, a five year sequence might yield the following number of fires each year: 2, 1, 0, 0, 2. Likewise, each farm fire started from a size that was the minimum of two numbers (see methods). As the number of farm fires each year increased, the likelihood of reaching 75% forest decreased, particularly above levels of two farm fires per year. This relationship interacted with farm fire size, with synergistic negative effects of increasing farm fire starting size and number of farm fires.

I detected a negative relationship between allowing burnt, unprotected land to be converted to farmland (variable importance = 4.95) and the likelihood of a landscape reaching 75% forest; this effect increased in size as the number of annual farm fires increased. Although the variable importance of protected land succession is low, it was the second most important interaction between variables detected (after an interaction between bird abundance interacting and mean LDD distance). The effect of land use was more apparent at moderate levels of average LDD. I consider this is likely due to the fact most areas of unprotected land were on the edges of the wetland, or in the middle, providing a 'stepping stone', reducing the separation of east and west areas of the wetland and between small forest fragments and the wetland (Figure 6.8). Therefore at the highest levels of average LDD distance, they may have been superfluous, whereas at the lowest levels of average LDD distance, they were unlikely to have made any difference. As for the effect of land use rules, if historic rates of fire

hold, the wetland is unlikely to be subject to more than 1 fire of the size range modelled, and in this parameter range (shaded in orange on Figure 6.7), variables such as average LDD distance swamp the effect of farm fire frequency.

Figure 6.8: Areas of the wetland that would revert to farmland after fire in some model scenarios are shown in white. These areas were private land in grass, shrub or forest at model initiation but were not within public conservation land, nor on private land but protected by conservation covenants.

What were the most important variables predicting the speed at which landscapes reached 75% forest?

Landscapes that reached 75% forest took a mean of 317 years to do so, but ranged from 162 to 500 years. I used boosted regression trees to test which parameters were associated with faster forest regeneration. I used only those landscapes which reached 75% forest, and used a Gaussian distribution for the response (time in years).

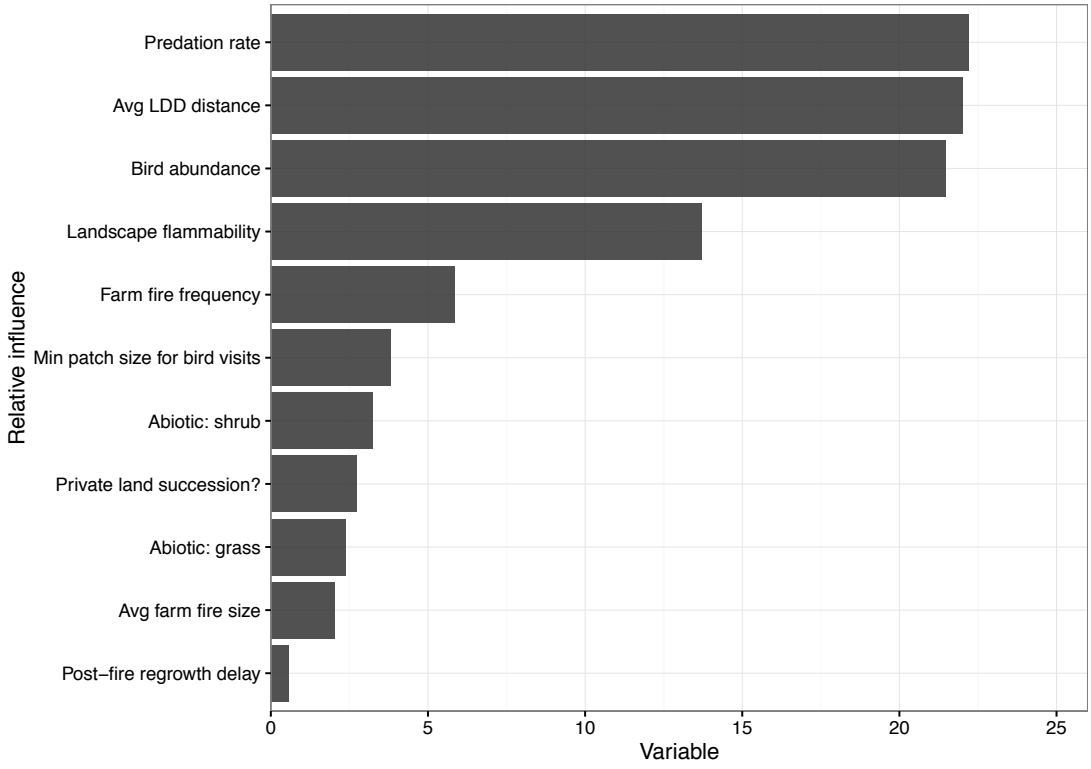


Figure 6.9: Relative variable importance of variables based on a boosted regression tree, testing which variables most influence length of time it takes landscapes to reach 75% forest. Relative important is based on how often variables among all regression trees (in this case, 10,910 iterations).

Unlike the analysis of whether a landscape would reach 75% forest (above, and Figure 6.5), variable importance was evenly split between the top three variables (Figure 6.9). Most important was predation rate (variable importance = 22.21), followed by average LDD distance (variable importance = 22.02) and bird abundance (variable importance = 21.47). Increases in the predation rate increased the length of time predicted for landscape to reach 75% forest. This was most evident at higher (700 – 1000 m) average LDD distances, where the predicted time increased rapidly after around 0.5 (or 50%) predation rate (Figure 6.10). It is likely this is because nuclei established but expanded slowly, creating isolated pockets of regeneration rather than large pockets that rapidly coalesce. Increases in average LDD distance decreased the time taken to reach 75% forest, but this effect was mediated by the predation rate (above) and by bird abundance. Low levels of bird abundance were associated with longer time to 75% forest and reduced the effect of increasing the average LDD distance (Figure 6.10).

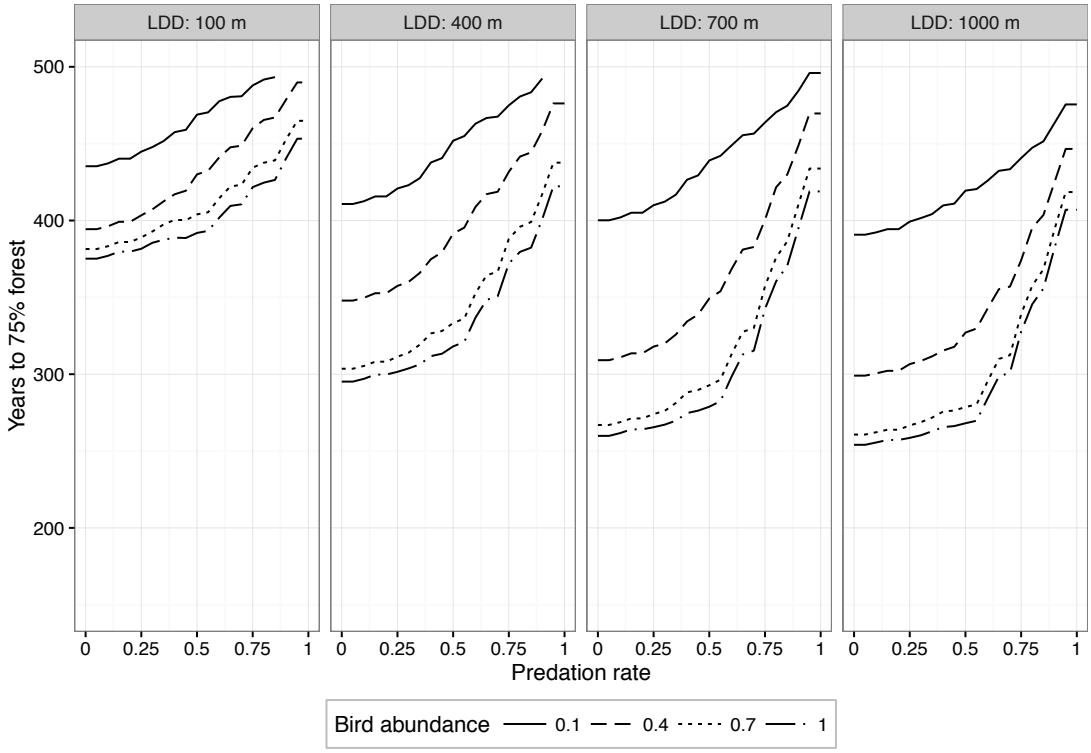


Figure 6.10: Predictions from boosted regression trees (n = 500 for prediction) exploring the interactions between average LDD distance ("LDD" in panel labels), bird abundance and the predation rate and their effects on the time it is predicted to take landscapes to reach 75% forest. All other variables are held at the mean for all simulations and predictions are truncated at 500 years (the extent of the data used to predict them).

The importance of landscape configuration and forest restoration methods

I tested the importance of the existing landscape structure and forest amount by running 192 unique parameter combinations of the average LDD distance, bird abundance, predation rate, and annual farm fires on five starting configurations, each repeated five times, for a total of 4,800 simulations. I fixed landscape flammability to a set constant (0.27) because of the limited number of replications. If more replicates were possible, it would be preferable to have varied it as for the sensitivity analysis. The starting configurations were:

1. the existing landscape used in the sensitivity model;
2. the existing landscape + 10% more forest, which replaced existing shrub, applied through nucleation as described;
3. the existing landscape + 10% more forest, which replaced existing shrub, added around the edges of existing forest remnants.

Examples of the landscapes used are provided in Figure 6.11.

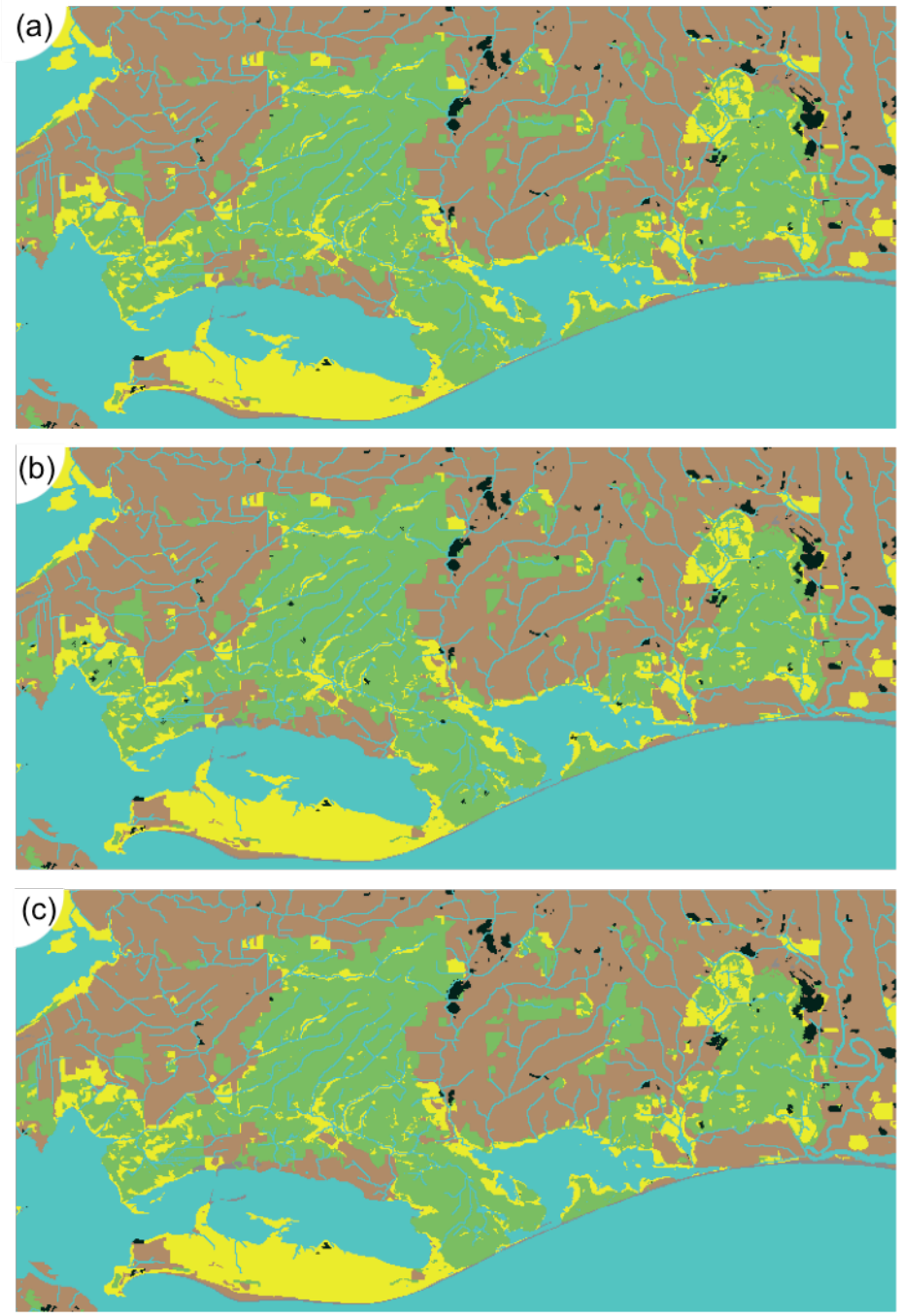


Figure 6.11: Landscape configuration options – example starting configurations. (a) The current starting configuration used in all sensitivity analysis. (b) The current landscape + 10% extra forest added as nuclei. (c) The current landscape + 10% added forest around the edges of existing forest remnants.

Does increasing the starting amount of forest increase the amount of forest?

The starting configurations were designed to differ in the amount and spatial arrangement of the forest patches.

Among the current landscapes (current, current + 10% nucleation, current + 10% edges), total area was increased (as planned) under the nucleation and edge treatments (Figure 6.12). The number of forest clusters (contiguous areas of forest) was higher in the nucleation compared to the edge and current treatments, which was as expected. The edge treatment caused some clusters to coalesce, meaning it had fewer distinct clusters than the current treatment. Mean 'core' (non-edge) patch area is calculated as the number of 'core' cells (NetLogo forest grid cells not adjacent to any patches with a vegetation type other than forest), divided by the number of forest clusters, and so gives an indication of the amount of 'core' habitat relatively independent of the amount of forest in the landscape. Mean core patch area was lowest in the nucleation treatment and highest in the edge treatment. This predicted, given the nucleation treatment increased forest by adding small clusters with an associated small amount of core patch area, and high edge area, whereas the edge treatment added forest by increasing the core-edge ratio of existing clusters. However, the absolute proportion of the landscape (in this case, the proportion of the landscape which was able to succeed to forest) in core area was higher in the nucleation treatment than the current treatment, because adding even small areas with low core to edge ratio still increases the absolute amount of core area. Again, the edge treatment had the greatest amount of core area (Figure 6.12).

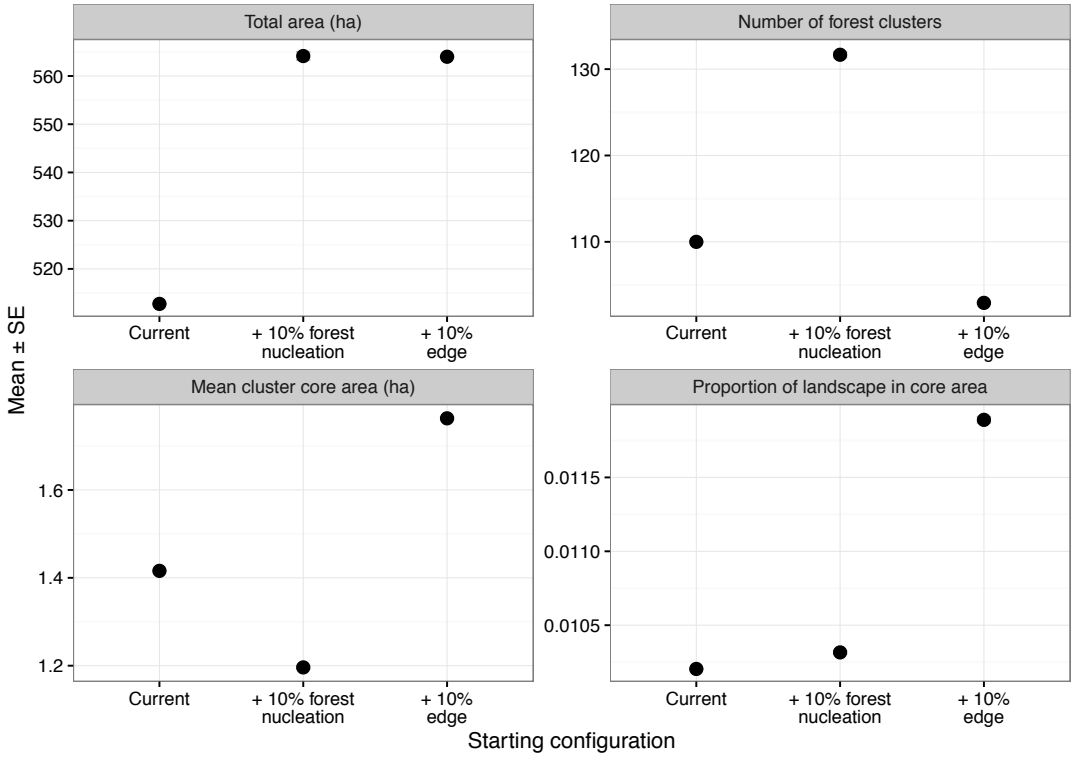


Figure 6.12: Comparison of spatial metrics (total area (ha), number of forest clusters, mean cluster core area (ha) and proportion of the landscape in core areas) between the current configuration and current configuration with added forest scenarios. A forest 'cluster' is a group of patches (each 50 x 50 m) of forest that are contiguous. The proportion of landscape in core area is calculated as the amount of core area as a proportion of the landscape that could succeed to forest under the vegetation transition rules. Standard error bars are masked by data points.

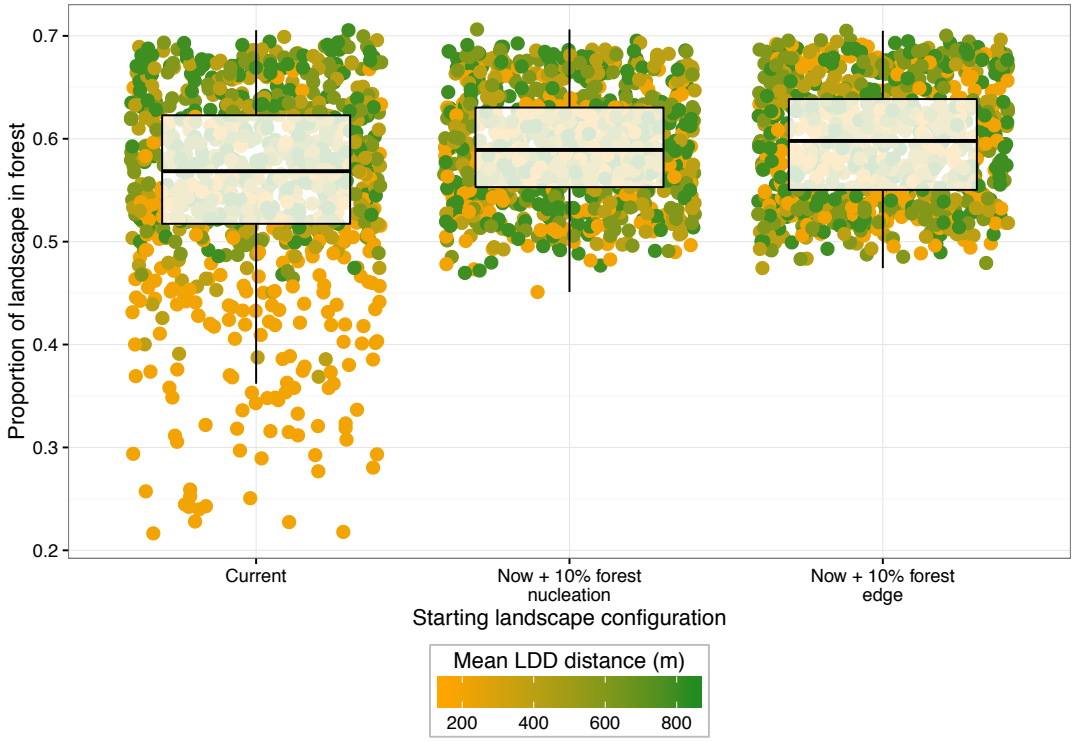


Figure 6.13: Boxplot of proportion of forest in n = 960 replicate runs of three starting configurations. The effect of the amount of forest and its configuration based on Awarua spatial models with varying levels of mean LDD distance, bird abundance, predation rate and annual farm fires. The current configuration (i.e., current configuration, current amount of forest) scenario is the same starting configuration used in the sensitivity analysis.

I tested whether adding forest to the current starting configuration (a) increased the amount of forest at the end of the model (500 years), (b) whether final forest amount differed between the method of forest addition (nucleation vs edge addition) and (c) whether increasing the amount of forest decreased the sensitivity of landscapes to average LDD distance, the most important variable in the sensitivity analysis. I tested these questions using a generalised linear mixed effects model (GLMM), using the proportion of forest remaining as the response variable, with fixed effects of starting configuration, average LDD distance, and an interaction between the two. I used a random intercept for each series (n = 5) with model realisation (n = 576 [192 unique parameter combinations multiplied by 3 starting configurations]) nested within it.

The "As now" starting configuration performed significantly more poorly than the model adding 10% forest in nuclei; there was no significant difference

between the “nuclei” and “edge” method (Table 6.1). The effect of average LDD distance (the key variable explanatory variable described in section (1)) was significant only for the “As now” starting configuration (Figure 6.14).

Table6. 1: The “As now” starting configuration is significantly improved in terms of the proportion of forest at model-end by adding 10% forest distributed in nuclei; there is no significant difference between the method of adding forest (+ 10% nuclei or +10% on edges). Mean long distance dispersal difference is not a significant predictor the proportion of forest at the end of the model for starting configurations with added forest; it is for the “As now” starting configuration. Average LDD distance values were divided by 10 prior to analysis.

Variable	Estimate	Std error	z value	p
Intercept	0.341	0.021	16.34	> 0.000
Starting configuration - As now	-0.535	0.03	-18.133	> 0.000
Starting configuration - +10% edges	0.036	0.03	1.226	0.22
Average LDD distance	0.033	0.019	1.722	0.085
Starting configuration - As now : Average LDD distance	0.391	0.027	14.498	> 0.000
Starting configuration - +10% edges : Average LDD distance	-0.012	0.027	-0.458	0.647

The mean forest proportion for each LDD distance value tested (200, 400, 600 and 800 m) is presented in Figure 6.14. The increase between 200 m and 400 m is consistent with the results of the sensitivity analysis (Figure 6.6).

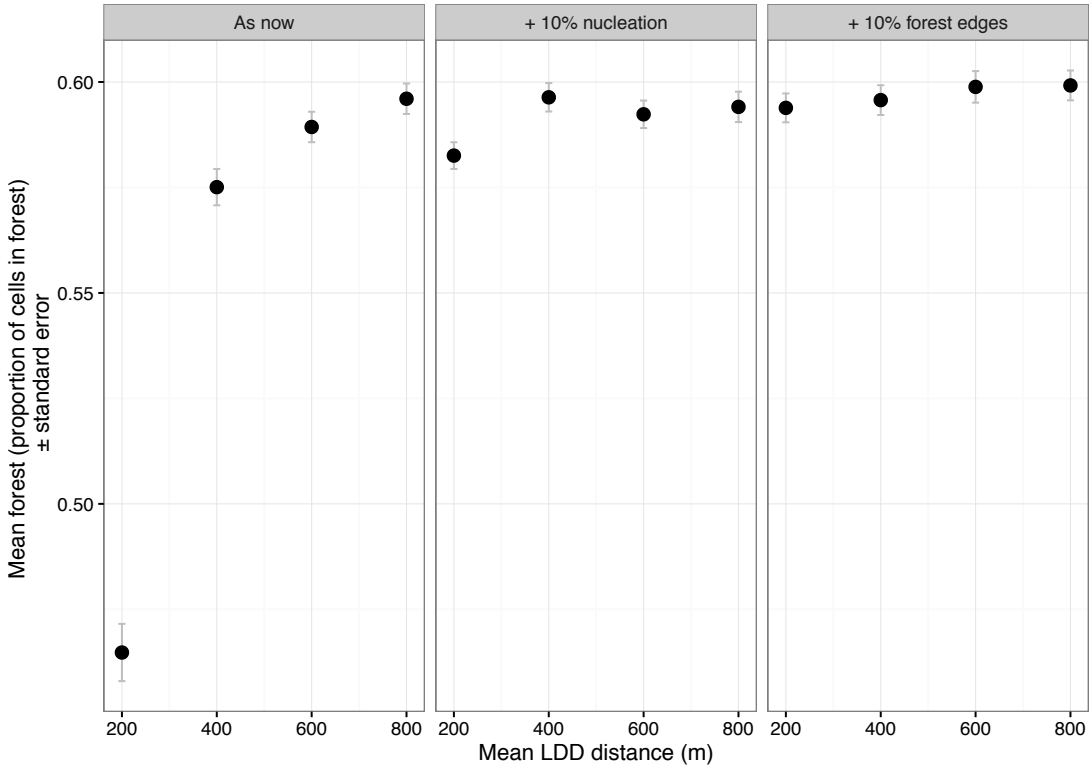


Figure 6.14: Starting configuration and average LDD distance interact to affect the proportion of forest remaining at 500 years. Data shown is raw data means with error bars indicating standard error around the mean, n = 240 for each data point.

6.4 Discussion

The importance of seed dispersal

Reliance on seed dispersal in the face of global bird declines has been recognised as a risk to plant persistence and spread (Şekercioğlu, Daily & Ehrlich 2004; Corlett 2007). In New Zealand, most (59%) trees rely on animal dispersal (Kelly, Ladley & Robertson 2004), and despite the extinction of 41% of the endemic forest bird species (Clout & Hay 1989; Innes *et al.* 2010), most plant-bird dispersal mutualisms remain intact (Kelly *et al.* 2010). However, even in the context of extant plant-bird mutualisms, colonisation of disturbed sites is disrupted by fragmentation (Wunderle 1997; Duncan & Chapman 1999; Holl 1999; Wijdeven & Kuzee 2000), and as discussed in Chapter 4, a lack of seed arrival is a common barrier to forest regeneration (Aide & Cavelier 1994; Holl 1999; Wijdeven & Kuzee 2000; Cubina & Aide 2001; Howe & Miriti 2004; Hooper, Legendre & Condit 2005; Kelm, Wiesner & Helversen 2008). As noted by

Wunderle Jr (1997) in a review of the role of animal seed dispersal for regeneration on degraded lands, the likelihood of seeds arriving by animal seed dispersal instead of active restoration efforts depends on landscape and ecosystem characteristics. These include the availability of a nearby seed source, the availability of animal seed dispersers, and the degree of the site's isolation. In New Zealand, Kelly *et al.* (2010) state there is a lack of knowledge about how much long distance dispersal is necessary for the maintenance of meta populations at the landscape scale.

This analysis highlighted the importance of dispersal, and particularly long distance dispersal, in highly fragmented landscapes. At Awarua, nearby seed sources are few, and the wetland is isolated from seed sources by the intensive agriculture that surrounds it. There were 2051 grid cells of forest in the model landscape, of a total of 154,924 terrestrial (non-water) grid cells (1.3%). This value is substantially below 30% historic cover, which has been postulated as a threshold for extinction debt is likely (Andren 1994), causing consequences for dispersers, and increasing the abundance of isolated, dispersal limited, pockets of forest (Hanski & Ovaskainen 2002). Variables relating to seed arrival at sites (average LDD distance and bird abundance) were the most important constraints on forest regeneration in the sensitivity analysis. They were the most influential variables on the likelihood of a landscape reaching 75% forest and were in the top three variables influencing the speed at which landscapes that reached 75% forest cover.

I tested whether active restoration techniques (planting forest seedlings) might increase the proportion of forest at the end of 500 years by either providing 'stepping stones' of forest from which natural regeneration can spread (known as 'applied nucleation': see discussion in Chapter 4 and Corbin and Holl (2012)), or by increasing the size of existing remnants. The lack of differences between the two methods suggests that forest quantity rather than spatial arrangement that will decrease reliance on long distance dispersal, and have the greatest contribution to forest regeneration. However, differences between methods

might arise as the proportion of forest added increases which would be a valuable avenue of further work.

The importance of predation, fire and land use

Although other studies have found seed predation and seedling herbivory to be the most important variable driving forest regeneration failure (Perry *et al.* 2015), differences to findings here can be reconciled. The process of regeneration at sites is sequential, that is, seeds must first arrive before they can pass through filters such as seed predation (Fattorini & Halle 2004). If very few or no seeds are arriving at sites, there is little scope for seed predation to have a negative effect. In models that attained 75% forest, the predation rate was the most important factor influencing the speed of forest regeneration. This sequential limitation is consistent with the seed sowing experiment (Chapter 2). There, I found low-dispersal sites were so seed-limited that we only detected seed predation and herbivory after artificially sowing seed, but after seed limitation was addressed, caging seeds and seedlings had the largest effect size on seedling survival and seedling biomass compared to other treatments.

Perry *et al.* (2015) found synergistic interactions between fire and invasive pyrophillic shrubs in a spatial model based on a northern New Zealand landscape, with a positive feedback between increased fire and shrub invasion. In the Awarua model, the mean number of annual farm fires was less important than variables associated with dispersal and predation. At current levels of 0-1 fires on average per year, the impact on the likelihood of forest regeneration and speed of regeneration is relatively low. However, each fire presents an opportunity for invasive pyrophillic shrubs to invade and catalyse a fire-trapped landscape, in which positive feedbacks occur between early-successional, flammable species and anthropogenic fire with the effect of stalled successions. The establishment of relatively flammable shrubs has occurred in Awarua with gorse (*Ulex europaeus*) and bracken (*Pteridium esculentum*) after fire (Johnson 2001), and these risks reflect those identified by Robertson and Suggate (2011). Extending the Awarua model to take account of these risks and interactions would be illuminating.

I discuss whether the applicability of the concepts of alternative stable states and stalled succession to the wetland's current state and likely trajectories in Chapter 7, in light of the spatial model discussed in this chapter, the experiments undertaken in Chapter 2.

Computational resources

Spatial models are limited by computational resources (Perry & Enright 2006) from covering too great an area, modelling in too fine detail, or requiring too many calculations (which will increase with both model complexity and number of modelled time steps). The Awarua models covered 555,842 ha on a 50 x 50 m grid and ran for 500 years, and took over 8,000 core hours on a supercomputer to run the sensitivity analysis and starting configuration analyses. Although it would be interesting to expand the spatial scope, or complexity, of the model, this would necessarily require a compromise in one of the elements of the model.

6.5 Conclusion

Exploratory spatial models can be useful where they plausibly demonstrate unexpected properties (Bankes 1993). The importance of long-distance dispersal and bird abundance was inconsistent with previous work but consistent across the responses tested for current landscape configurations. The reduction in reliance on long distance dispersal following the addition of 10% extra forest at model initiation (51.25 ha) suggests that it is the paucity of forest in the landscape driving these effects. Given observed dispersal limitation within Craws Creek, Awarua (Chapter 2), findings here indicate regeneration may stall due to a lack of bird dispersal. Given the constraints of bird dispersal limitation and seed predation and seedling herbivory are sequential, I consider active restoration efforts will be a more effective route than attempting to rely on existing levels of long-distance dispersal, and that control of invasive mammals which eat seeds and seedlings is likely to speed regeneration, but only after seed limitation is addressed. It is not possible to accurately predict the likelihood of the real Awarua wetland reaching 75% forest within 500 years based on the spatial model. However, prioritisation of active management based on its findings would be beneficial, and consistent with the recommended actions based on fieldwork in Chapter 2.

Appendix 6.1: Overview, Design Concepts and Details of spatial model

This document is based on the template in "The ODD protocol: a review and first update" by Grimm *et al.* (2010), but only includes aspects of the template that are relevant to this model.

1. Purpose

The model is designed to explore the interaction between constraints to forest regeneration with-in the Awarua catchment. In particular, I sought to quantify the importance of dispersal; land use, predation/herbivory and anthropogenic fires to forest regeneration.

2. Entities, state variables, and scales

Parameter sweep model (n = 2000)

Variable	Description	Values	Source	Scale	Effect
General					
Landscape size	681 * 327 cells	NA	NA	NA	NA
Cell size	50 * 50 m	NA	NA	NA	NA
Model duration	500 years	NA	NA	NA	NA
Spatial units					
Vegetation type	Existing vegetation cover	forest; shrub; grassland; farmland; water (excluding rivers)	LCDB/Boffa Miskell mapping	Polygons rasterised to 50 x 50 m grid	Vegetation types have specific flammability values
River	Whether a cell includes a river	true/false	New Zealand river centrelines from the LINZ 1:50,000	Applied as lines in ARCGIS; read into netlogo; where a river 'intersects' a patch that patch is river =	Rivers reduce the flammability of cells they pass through, but are considered too wet to hold forest

			NZTopo database.	TRUE	
Protected	Whether or not land is protected by being held by the Government (DOC) or as a scenic/scientific reserve; private land in QEII covenants also qualifies	true/false	QEII (2011) and land tenure data from Department of Conservation (Southland Conservancy)	NA	NA
Fire					
Flammability	Landscape flammability value	0 - 1	NA	NA	Increases flammability of patches based on vegetation type
Rate of farm fires	Number of farm fires per year	0 - 4	Range based on historic fire data supplied by Southland District	NA	Direct effect on number of fire per year

			Council, with thanks to Southland Rural Fire Authority		
Farm fire size	Mean (to draw from a poisson distribution) of farm fire once it reaches edge of wetland	4 - 28	Massive guess	NA	Affects size of fires each year (in patches)
Herbivory					
Herbivory/predation rate	Amount of pre-dispersal seed predation and seedling herbivory	0 - 1	NA	NA	Reduces seedlings available to be dispersed. Increases mortality of existing seedlings
Landuse					
Protected land regrows?	Whether unprotected land (not in QEII covenants or government land) will revert to grassland if burnt	TRUE/FALSE	NA	NA	Unprotected land reverts to farmland if burnt
Dispersal					
Bird	Relative abundance of birds in the landscape	0 - 1	NA	NA	Lower numbers

abundance					decrease percolation regeneration and LDD
Mean bird dispersal distance	Mean value (drawn from random exponential distribution) LDD event will go	0 - 20	Generalised from Wotton & Kelly (2012)	Patches; 50 m patches = max of 1 km	Mean distance of each LDD event, higher means LDD events travel further
LDD threshold	Threshold value - minimum forest cluster size below which frugivorous birds won't visit	0 - 8 grid cells	NA	NA	"Clusters" of forest below the threshold are not considered by birds for visitation, and therefore no seeds are dispersed from them
Abiotic parameters					
Gmax	Minimum period (in years) until grassland can transition to shrub	0 - 50	Rogers (1994)	NA	High values slow the transition from grassland to shrub
Smax	Minimum period (in years) until shrub can transition to forest	50 - 120	Allen, Engeman and Krupa (1996), Williams and	NA	High values slow the transition from shrub to forest

			Karl (2002)		
Lag	Number of years post-fire until grassland establishs	1 - 4	Varied in models. For case studies set to 1 year (Johnson (2001))	NA	High values leave burnt ground bare for longer

Starting configuration model (total simulations = 4800, each scenario number of simulations = 5, number of unique parameter combinations in each scenario = 960)

In these models I used three different starting configurations:

1. Existing landscape
2. Existing landscape + 10% extra forest (forest added to edges of existing remnant)
3. Existing landscape + 10% extra forest (forest added in small nucleii randomly placed in landscape)

Variable	**Value**
Herbivory/predation rate	0.2, 0.4, 0.6, 0.8
Bird abundance	0.2, 0.4, 0.6, 0.8
Mean bird dispersal distance	4, 8, 12, 16
Rate of farm fires	0.5, 1, 1.5

	Percentage of vegtype in landscape (excluding water)			
Starting state	*Forest*	*Shrub*	*Grass*	*Farmland*
Current proportions	1.83	4.32	19.84	74.00
Current + 10%	2.01	4.14	19.84	74.00

3. Process overview and scheduling

After model setup (described above), the following processes occur, which are described below.

1. Local seed dispersal
2. Long-distance seed dispersal
3. Vegetation transition
4. Lightning fires
5. Farm farms

Local seed dispersal

Forest grid cells and shrub grid cells which have received forest seed and whose seedlings are more than 15 years (seedling age) are seed sources (qualifying patches) for nearby dispersal. The qualifying patches are multiplied by the bird abundance (because smaller bird populations mean not all patches will be receiving dispersal services). Shrub patches which are immediately adjacent (nearest four neighbouring patches) and more than 25 years old can receive forest seeds (seed receivers). Seed receivers receive seeds weighted by the number of forest patches and shrub patches (shrub patches produce half the seeds that mature forest patches do). The number of seeds received is reduced by multiplying the number of seeds by 1 – predation rate. For seed receivers that have not received forest seeds before, the seedling age counter is initiated. For seed receivers that have received forest seeds before, seedling age is increased by one.

Long-distance seed dispersal

Long distance dispersal is only potentially initiated in forest patches for whom the count of their forest neighbours is above the visitation threshold (LDD threshold), and neighbouring forest patches to avoid excluding edge forest patches on qualifying forest cluster (qualifying LDD patches).

The number of patches that will be visited by birds is multiplied by the bird abundance (number of dispersing patches), meaning that lower bird abundance values will result in fewer patches having seeds dispersed. The patches dispersing seed are randomly selected from all qualifying LDD patches, and each selects a patch (target patch) by choosing a random direction (between 0 and 360 degrees), and a distance drawn from an exponential distribution with a mean of x, x being the mean bird dispersal distance (above). If the target distance and direction caused the target to be 'off' the model, then those seeds were regarded as having been 'lost' to the landscape and they had no effect on the model.

If the target patch is a shrub patch, it receives the same amount of seeds as if it were receiving local scale seed dispersal from a forest patch, multiplied by 1 – predation rate. For seed receivers that have not received forest seeds before, the seedling age counter is initiated. For seed receivers that have received forest seeds before, seedling age is increased by one. The number of seedlings received by each patch (as modified by the predation rate) were recorded, as it affected the likelihood of shrub transitioning to forest.

Vegetation transition

At each time step, each path is evaluated and will transition to another vegetation type if criteria are fulfilled:

- Burnt ground will transition to farmland or grass after a constant amount of time (variable "lag", above) has passed. Land that was farmland prior to being burnt will always return to farmland; grass will always return to grass in protected areas. In unprotected areas grass either returns to grassland or farmland, depending on the modelled scenario.
- Grassland will transition to shrub where: the minimum amount of time – a constant "Gmax" (above) has passed; the patch is not in a river cell; and where a random number with a maximum value of 1 is less than 0.01 (to stagger transitions initially and after large scale disturbance events.
- Shrub will transition to forest where: the minimum amount of time – a constant "Smax" (above) has passed; the patch is not in a river cell; the patch is not in the "shrub set back zone", which includes all patches with rivers, all patches with more than one neighbour in the neighbouring 8 cells with a river, and patches for whom roads pass through; and a random number between 0 and 100 is smaller than the number of seeds it has received.
- The flammability of each patch is recalculated each turn and is influenced by whether a river flows through the patch (reduces flammability) and the flammability of surrounding patches, if that increases the flammability of the patch.

Lightning fires

Lightning is parameterized with the modelled natural lightning rate for New Zealand (Etherington 2015, pers comm). Lightning strikes were calculated based on the size of the landscape to be a mean of 38.97 with a standard deviation of 11.69 across the whole landscape. Each turn the number of lightning strikes is drawn from a normal distribution. A patch will ignite when struck by lightning depending on its flammability and random chance. If a patch ignites, the fire then spreads according to percolation theory.

Farm fires

Farm fires are not meant to represent anthropogenic fire in the landscape; instead, they are meant to depict how many risky fires occur near the wetland each year. Each year the number of such fires is drawn from a Poisson distribution with the mean set by the constant variable annual farm fires (above). Farm fires ignite in patches with at least one patch of forest, shrub or grass with-in a radius of 2 patches. The size of the fire is drawn from a Poisson distribution with the mean set by the constant variable farm fire size, with a ceiling of the number of flammable patches (forest, shrub, grassland, farmland) within a radius of 4 patches. A patch will ignite when a neighbour is on fire depending on its flammability and random chance. If a patch ignites, the fire then spreads according to percolation theory.

4. Design concepts

Emergence

Some elements of the models are expected to vary in complex and perhaps unpredictable ways when particular characteristics of individuals or their environment change. “Hot spots” of flammability or fire may emerge in local areas due to vegetation transitions and ‘leaky’ patch flammability. Hotspots might also be driven by high degree of variation in farm fire size and randomized ignition points that may lead to several large fires in the same area for successive years. Depending on the protected land transition rules, forest or shrub may be

"lost" from the model at any time when unprotected land reverts to farmland, which may have disproportionate effects depending on how crucial the area was as a 'stepping stone' for bird dispersal.

Stochasticity.

The processes of dispersal, vegetation transition, lightning strikes, farm fires all included elements of stochasticity. Long distance dispersal occurs from randomly selected cells (where not all qualifying cells disperse) and receiving cells are chosen from a random direction and a randomly generated distance (although with constant mean in each model). Local dispersal is less stochastic, but again, where bird abundance is below 1, grid cells are randomly select to undertake local dispersal. The location of lightning strikes and farm fires varies randomly each turn, and the likelihood of a neighbouring patch igniting is also subject to an element of random chance. Finally, even within vegetation transition, there is an element of random chance involved in the transitions of grass to shrub, and shrub to forest.

5. Initialization

The models were always initialised in the same state, except for the parameters which were varied and have been described above.

In the starting state sub-models the landscape configuration was changed. For the current landscape configuration with added forest this was as described above. For randomized landscape configurations the starting clusters were initiated with a random seed. Each iteration of the model used a new landscape (either forest was increased at random, according to the constraints of where it could potentially go, or the random habitat clusters in the landscape were recalculated.

Chapter Seven: Conclusions

The main objective of my thesis was to quantify constraints to native forest regeneration within Awarua wetland. There are multiple constraints which apply sequentially and at different scales (Figure 7.1). Additionally, constraints interact, making it hard to evaluate them in isolation. In this chapter I attempt to evaluate the relative importance of the four most important factors, and then apply this evaluation to answering firstly, whether there is evidence of alternative stables states or a stalled succession at Awarua, secondly, whether active restoration is required, and thirdly, and based on the answer to the first and second questions, whether an entry on the Montreux Record under the Ramsar Convention is likely to be required for the wetland.

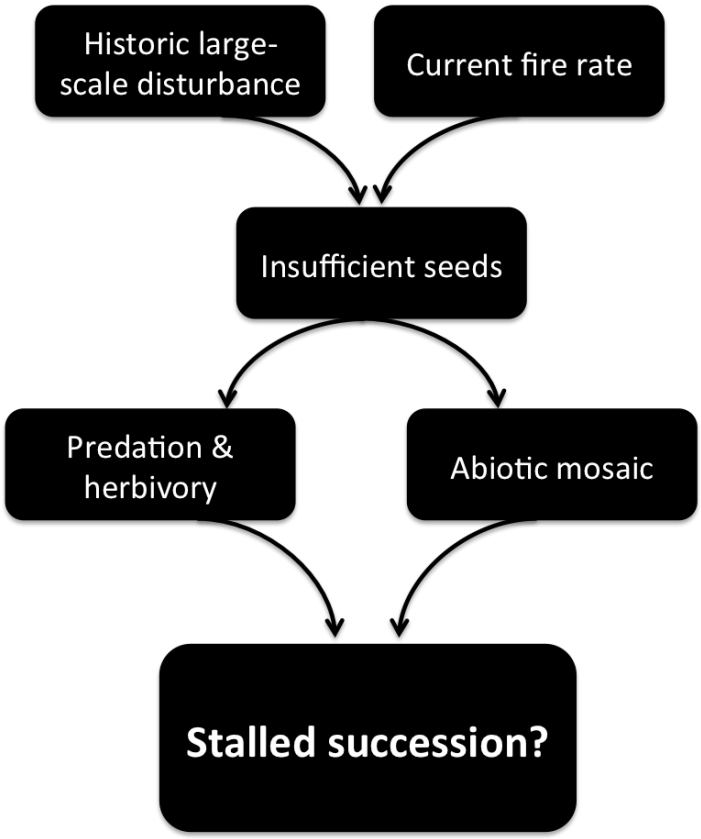


Figure 7.1: At the landscape level, historic disturbance and the current rate of anthropic fire has driven the fragmentation of forest fragments within the Awarua catchment and reset regeneration within the wetland, leaving it vulnerable to invasion by exotic, highly flammable species. If seed addition is addressed, predation and herbivory, and the abiotic environment, might still slow regeneration, thus still resulting in a stalled succession.

7.1 Constraints to forest regeneration in Awarua

Dispersal

I found that there were few forest fragments within the wetland catchment (Chapter 7) and that the wetland was seed limited (seed sowing experiment, Chapter 2). Even where there are seed sources nearby, it appeared there was a lack of birds undertaking effective dispersal within the wetland (vegetation survey and seed trapping experiments, Chapter 2), as the number of seedlings and total plot biomass (summed plant heights) dropped steeply at > 230 m from the centre of a forest remnant, and less than half the species found in seed traps within the forest remnant were caught as seeds in seed traps in adjacent mānuka.

Seed germination and establishment

If seeds were to arrive in the mānuka areas of the wetland, most areas would be abiotically suitable for seeds to establish. Mānuka was relatively slow growing in the wetland (Introduction, Chapter 5), and will likely become more suitable for seed establishment as it self-thins and allows more light in through the canopy (seed sowing experiment, Chapter 2). I did not obtain conclusive evidence of whether seeds were likely to establish in red tussock areas if dispersed naturally or sown via direct seeding, as only one species germinated (sowing experiment, Chapter 5). If seeds arrive they are likely to be reduced in number by predation (seed sowing experiment, Chapter 2 and sowing experiment, Chapter 5), and if they establish as seedlings, they are likely to have biomass reduced by predation herbivory (seed sowing experiment, Chapter 2).

Seedling growth

Plants planted into the wetland as established seedlings survived relatively well, and were more resilient to the effects of herbivory (Chapter 5) compared to seeds (Chapter 2). Mānuka appeared to confer more benefits as a nurse species in terms of protection from excessive solar radiation than *Chionochloa rubra*, an alternative nurse species, although both nurse species were able to establish where one forest species (*Carpodetus serratus*) was not. *Carpodetus serratus*

seedlings were subject to an apparent abiotic threshold, unable to survive where the mean groundwater table was too high.

Fire

Fire is correlated with the historic loss of later-successional native forest within the wetland (Wilmshurst, J., 2015, pers comm.). Considering the slow growth rate of mānuka, it may take a century for later-successional forest to establish under mānuka. The rate of this regeneration is probably similar to regeneration after small-scale historic disturbance, such as lightning fire, however the landscape context and abiotic environment is quite different to pre-human times. The lack of seed sources in the landscape and seed predation and herbivory combine to slow or stall the 'natural' rate of regeneration, meaning forest regeneration will require more effective fire-prevention efforts than has happened to date at current fire sizes and frequencies; and may not be possible given the surrounding agricultural land uses.

7.2 Is there evidence of alternative stable states at Awarua?

Alternative stable state theory predicts that different ecosystems may persist indefinitely under the same environmental conditions (Schröder *et al.* 2005). Evidence of alternative stable states is usually found by monitoring a system after a disturbance has ceased (Beisner, Haydon & Cuddington 2003).

Alternative stable states are often characterised by hysteresis, that is, a state change from state A to state B may occur at a certain parameter value but the return does not occur at the same parameter value (Beisner, Haydon & Cuddington 2003).

The concept of alternative stable states has been applied to restoration ecology (Suding & Hobbs 2009); evidence has been found where fragmentation and seed limitation combine to drive alternative stable states after disturbance in Australian old-fields (Standish *et al.* 2007) and in broom-invaded areas (Wearne & Morgan 2006); alternative states have also been driven by exotic herbivores (Holmgren 2002). The replacement of one state by another needs a disturbance

that induces a set of positive feedback mechanisms (Wilson & Agnew 1992; Petraitis & Latham 1999). Although it can be difficult to meet a strict definition of indefinite persistence, the concept of alternative stable states can be useful for evaluating whether states are self-reinforcing (Suding, Gross & Houseman 2004).

Petraitis and Latham (1999) note that although alternative stable states can be tested in marine systems, switches between forests and heathlands are too large to test experimentally. However, alternative stable states have been documented at a large-scale. In Australia, clearance of deep-rooted vegetation and replacement by shallower-rooted crops led to decreased interception of soil water, and subsequently, the rise in groundwater levels and an upwelling of mobilised salt (Cramer & Hobbs 2002), leading to irreversible changes where deep-rooted vegetation can no longer establish (Hobbs, Cramer & Kristjanson 2003). By 2050, it has been predicted more than 2 million ha may be affected by salinization (Cramer & Hobbs 2002).

Disturbances to force a switch to an alternative state need to be large enough (in geographic extent and impact) to allow a sufficient window of opportunity for invasion of individuals of species which will compose the alternative state (Petraitis & Latham 1999). Switches of such a scale have been explored using spatially-explicit models (Perry & Enright 2002). Stalled (or arrested) successions are successions that require active management interventions to recover a natural trajectory and being in a stalled succession may make a system more vulnerable to alternative stable states (Ghazoul *et al.* 2015). Human timeframes can make it difficult to differntiate between alternative stable states, stalled successions and slow natural regeneration – as an example, cultivated fields abandoned in late mediaeval times on a trajectory to natural grasslands may still be at an early succession stage, and similar grasslands have been suggested to be succeeding at the same rate as woodlands (Gibson & Brown 1991).

To place Awarua within the conceptual framework of alternative stable states and arrested successions, we need to consider which possible states the wetland

could assume, under current environment conditions. We know that historically the wetland is likely to have been forested, becoming mānuka dominated only after substantial human fires and clearance. The wetland is suitable for forest in most areas of mānuka (Chapter 2, sowing experiment), and potentially areas of *Chionochloa rubra* (Chapter 5, planting experiment). We know that in some areas there are abiotic thresholds to seedling establishment and survival (Chapter 5, planting experiment), suggesting the wetland could support a mosaic of shrubland, grassland and later successional forest as in historic times. At present, the system is dominated by shrubland (primarily mānuka), with other community types, such as *C. rubra* and flax (*Phormium tenax*) in wetter areas (Anon. 2010).

For the purposes of discussion, I define "current environmental conditions" to be equivalent to the fundamental niche (Chapter 1), which excludes current biotic conditions and the disturbance regime (fire). There are three possibilities with regard to alternative stable states:

1. The system is being observed at the mid-point in a succession trajectory which will inevitably lead to a forest mosaic (one stable state – forest dominated): any dominance by shrub species is too temporary to be considered an alternative *stable* state, and it is merely the long, slow process of natural regeneration;
2. Current conditions no longer reflect historic conditions (e.g. a change in hydrology) and it is not possible to return to a forest-dominated mosaic (one stable state – shrubland);
3. There are multiple stable states that could exist under current conditions: a flammable shrubland (native or exotic) dominated system, and a forest dominated mosaic. Which state emerges and persists will depend on biotic conditions and the disturbance regime;
4. An additional possibility is that, although no alternative stable states have been identified, and in contrast to the first option, regeneration will not occur without active management, in which case the term 'stalled succession' would most accurately apply.

The wetland is relatively wet (high water table) and acidic, but mānuka has dominated, and invasive shrubs have been able to establish, ruling out option 1. At the very least, in the absence of seed inputs, the wetland is likely to remain in mānuka which may take the unusual step of self-replacing at the end of its natural lifespan, as can happen where forest does not establish (Dobson 1979; Wardle 1991). I demonstrated in Chapter 2 that when seed limitation is addressed, the wetland is capable of supporting forest, which rules out option 2. Shrub species are capable of persisting in the wetland and are unlikely to be invaded by forest without any external seed inputs, which is exacerbated by lack of long-lived seed banks in New Zealand (Enright & Cameron 1988). Therefore, mānuka-shrubland is capable of being an 'alternative' state, although insufficient time has passed for a definitive diagnosis. If invasive shrubs were to invade and particularly if they influenced the rate or spread of fires, this could also be considered an alternative state. The multiple interacting constraints to regeneration I found, in combination with the forest-depauperate landscape context indicates the wetland is in a stalled succession, and as a whole, is unlikely to become forest dominated without active management. Overall, I consider there are multiple future potential states, and that the wetland is vulnerable to flipping to an alternative state. However, it is too soon to draw the conclusion an alternative stable state has established, until either mānuka self-replaces, fires continue, or exotic shrubs invade.

7.3 Are active restoration actions required?

Having reached the conclusion the wetland is in a stalled succession (above), active management, if not active restoration (Chapter 1 – active restoration is not generally considered to include actions which involve the cessation of activities or constraints) could be necessary. Fires are a relatively regular occurrence within the wetland. To speed regeneration and decrease how long the wetland is this vulnerable to fire, active restoration efforts are probably necessary to reduce the seed and dispersal limitation within the wetland. I quantified the costs and benefits of active restoration actions within the wetland

(Chapter 4). I found that seeds and seedling planting will successfully establish forest species in the wetland, unlike bird perches (Chapter 4). Seeds are cheaper and quicker to disperse, but are much smaller and more vulnerable to seed predation and herbivory. Based on planted seedlings' greater resilience to herbivory, and because I found evidence of possums everywhere I tested within the wetland (Chapter 3), I consider that plants grown to 2- or 3- years old in a nursery would be a good choice for restoration efforts.

7.4 Is a notification under the Ramsar convention likely to be required for ecological character change?

Parties to the Ramsar Convention are expected to manage listed wetlands such that their ecological character is maintained (Article 3.1, Ramsar Convention). Awarua is a listed wetland under the Ramsar convention, which requires New Zealand, as a contracting party, to inform the secretariat if any qualifying negative change in ecological change occurs. Ecological character has been defined as (Ramsar Convention 2005a, Resolution IX.1 Annex A, COP9):

> *The combination of the ecosystem components, processes and benefits/services that characterise the wetland at a given point in time*

Change in ecological character has been defined as (Ramsar (2005): COP 9 Resolution IX.1 Annex A):

> *The human-induced **adverse** alteration of any ecosystem component, process, and/or ecosystem benefit/service*

Australian national guidance (Department of the Environment Water Heritage and the Arts 2009) suggests that the fact that a site was not in pristine condition, or was even undergoing change at the time of designation, does not preclude the need for assessment and potential listing. This is due to the fact that many wetlands were subject to adverse human-induced change at the time of designation. Where wetlands are on a change trajectory, the condition is expected to be maintained or restored (Department of the Environment Water

Heritage and the Arts 2009). Changes in ecological character only qualify under Article 3.2 if the change is negative, and human-induced. This is to allow for positive changes in ecological character, and to avoid highlighting inevitable, unavoidable changes in ecological character respectively. There is no guidance in the convention on how to distinguish human-induced change from natural change, such as where fires may be the accidental result of human land use; or in the case of omissions, such as a failure to control invasive species.

Although a detailed policy consideration is outside the scope of this thesis, ecological character change is measured against the character at time of designation, and any described limits to acceptable change (set by site managers). Where a site is reported it is placed on the Montreux Record, the purpose of which is to highlight sites in need of priority conservation attention (Guidelines for operation of the Montreux Record, adopted by CoP 1996, Resolution VI.1).

Invasive species have been recognised as a threat to ecological character (Ramsar (2002): COP 8 Resolution VIII18). The current state of the terrestrial areas of Awarua is unlikely to qualify as an adverse change to its ecological character, given a natural process of succession and regeneration was occurring at the time of designation. As with the answer to the question of alternative stable states, an adverse change may be beginning now; with forest regeneration currently inhibited and the potential for invasive species to establish; this is why preventative active restoration efforts are suggested.

7.5 Conclusions

Overall, it appears the wetland currently has the potential for either forest, a second generation of native shrubland, or an invasion of exotic shrubland, and that current and future management efforts are capable of influencing this trajectory towards more favourable future states.

References

(1971) Convention on Wetlands of International Importance especially as Waterfowl Habitat. As amended by the Paris Protocol, 3 December 1982, and Regina Amendments, 28 May 1987. Ramsar (Iran).

Aaron, G.B., Gullison, R.E., Rice, R.E. & Fonseca, G.A.B.d. (2001) Effectiveness of Parks in Protecting Tropical Biodiversity. *Science,* **291,** 125-128.

Adams, A.A.Y., Stanford, J.W., Wiewel, A.S. & Rodda, G.H. (2011) Modelling detectability of kiore (*Rattus exulans*) on Aguiguan, Mariana Islands, to inform possible eradication and monitoring efforts. *New Zealand Journal of Ecology,* **35,** 145-152.

Aide, T.M. & Cavelier, J. (1994) Barriers to Lowland Tropical Forest Restoration in the Sierra Nevada de Santa Marta, Colombia. *Restoration Ecology,* **2,** 219-229.

Aitchison, J. (1955) On the Distribution of a Positive Random Variable Having a Discrete Probability Mass at the Origin. *Journal of the American Statistical Association,* **50,** 901-908.

Albornoz, F., Gaxiola, A., Seaman, B., Pugnaire, F. & Armesto, J. (2013) Nucleation-driven regeneration promotes post-fire recovery in a Chilean temperate forest. *Plant Ecology,* **214,** 765-776.

Allen, R., Partridge, T., Lee, W. & Efford, M. (1992) Ecology of Kunzea ericoides (A. Rich.) J. Thompson (kanuka) in east Otago, New Zealand. *New Zealand Journal of Botany,* **30,** 135-149.

Allen, R., Payton, I. & Knowlton, J. (1984) Effects of ungulates on structure and species composition in the Urewera forests as shown by exclosures. *New Zealand Journal of Ecology,* **7,** 119-130.

Allen, R.B., Lee, W.G. & Rance, B.D. (1994) Regeneration in indigenous forest after eradication of Norway rats, Breaksea Island, New Zealand. *New Zealand Journal of Botany,* **32,** 429-439.

Andren, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos***,** 355-366.

Anon. United States of America Central Intelligence Agency The World Factbook.

Anon. (2010) Awarua Waituna Wetlands Hydrology and Vegetation Mapping Boffa Miskell Ltd and Urtica Inc.

Ausseil, A., Gerbeaux, P., Chadderton, W., Stephens, T., Brown, D. & Leathwick, J. (2008) Wetland ecosystems of national importance for biodiversity: Criteria, methods and candidate list of nationally important inland wetlands. Landcare Research New Zealand Limited and Department of Conservation, New Zealand.

Bachelet, D., Lenihan, J.M., Daly, C. & Neilson, R.P. (2000) Interactions between fire, grazing and climate change at Wind Cave National Park, SD. *Ecological modelling,* **134,** 229-244.

Baddeley, C.J. (1985) Assessments of wild animal abundance. *Forest Research Institute Bulletin,* **106,** 1-46.

Baeza, M., De Luıs, M., Raventós, J. & Escarré, A. (2002) Factors influencing fire behaviour in shrublands of different stand ages and the implications for using prescribed burning to reduce wildfire risk. *Journal of Environmental Management,* **65,** 199-208.

Baker, W.L. & Mladenoff, D.J. (1999) Progress and future directions in spatial modeling of forest landscapes. *Spatial modeling of forest landscape change. Cambridge University Press, Cambridge, UK***,** 333-349.

Ball, M.C. (1994) The role of photoinhibition during tree seedling establishment at low temperatures. *Photoinhibition of photosynthesis: from molecular mechanisms to the field***,** 365-376.

Banasiak, S. & Meiners, S. (2009) Long term dynamics of *Rosa multiflora* in a successional system. *Biological Invasions,* **11,** 215-224.

Bankes, S. (1993) Exploratory modeling for policy analysis. *Operations Research,* **41,** 435-449.

Bartoń, K. (2014) MuMIn: Multi-model inference.

Bates, D., Maechler, M., Bolker, B.M. & Walker, S. (2014) lme4: Linear mixed-effects models using Eigen and S4.

Beisner, B.E., Haydon, D.T. & Cuddington, K. (2003) Alternative stable states in ecology. *Frontiers in Ecology and the Environment,* **1,** 376-382.

Belsky, A.J. (1994) Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. *Ecology,* **75,** 922-932.

Benayas, J.M.R., Bullock, J.M. & Newton, A.C. (2008) Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. *Frontiers in Ecology and the Environment,* **6,** 329-336.

Bestelmeyer, B.T., Moseley, K., Shaver, P.L., Sanchez, H., Briske, D.D. & Fernandez-Gimenez, M.E. (2010) Practical Guidance for Developing State-and-Transition Models. *Rangelands,* **32,** 23-30.

Birch, J.C., Newton, A.C., Aquino, C.A., Cantarello, E., Echeverría, C., Kitzberger, T., Schiappacasse, I. & Garavito, N.T. (2010) Cost-effectiveness of dryland forest restoration evaluated by spatial analysis of ecosystem services. *Proceedings of the National Academy of Sciences,* **107,** 21925-21930.

Bivand, R.S., Pebesma, E. & Gomez-Rubio, V. (2005) Classes and methods for spatial data in R.

Blackwell, G.L., Potter, M.A. & McLennan, J.A. (2002) Rodent density indices from tracking tunnels, snap-traps and Fenn traps: do they tell the same story? *New Zealand Journal of Ecology,* **26,** 43-52.

Bonanomi, G., Incerti, G. & Mazzoleni, S. (2011) Assessing occurrence, specificity, and mechanisms of plant facilitation in terrestrial ecosystems. *Plant Ecology,* **212,** 1777-1790.

Bonilla‐Moheno, M. & Holl, K.D. (2010) Direct seeding to restore tropical mature forest species in areas of slash‐and‐burn agriculture. *Restoration Ecology,* **18,** 438-445.

Bray, J.R., Burke, W.D. & Struik, G.J. (1999) Propagule dispersion and forest regeneration in *Leptospermum scoparium* (manuka) – *L. ericoides* (kanuka) forests following fire in Golden Bay, New Zealand. *New Zealand Natural Sciences,* **24,** 35-52.

Brown, B.J. & Ewel, J.J. (1987) Herbivory in complex and simple tropical successional ecosystems. *Ecology***,** 108-116.

Brown, J.H., Stevens, G.C. & Kaufman, D.M. (1996) THE GEOGRAPHIC RANGE: Size, Shape, Boundaries, and Internal Structure. *Annual Review of Ecology and Systematics,* **27,** 597-623.

Brown, K.P., Moller, H., Innes, J. & Alterio, N. (1996) Calibration of tunnel tracking rates to estimate relative abundance of ship rats (*Rattus rattus*) and mice (*Mus musculus*) in a New Zealand forest. *New Zealand Journal of Ecology,* **20,** 271-276.

Brown, S. & Lugo, A.E. (1990) Tropical secondary forests. *Journal of tropical ecology,* **6,** 1-32.

Bulleri, F., Bruno, J.F., Silliman, B.R. & Stachowicz, J.J. (2015) Facilitation and the niche: implications for coexistence, range shifts and ecosystem functioning. *Functional Ecology***,** n/a-n/a.

Burney, D.A. & Burney, L.P. (2007) Paleoecology and "inter-situ" restoration on Kaua'i, Hawai'i. *Frontiers in Ecology and the Environment,* **5,** 483-490.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multi-model inference: a practical information-theoretic approach*. Springer Verlag.

Burrows, C. (1973) The ecological niches of Leptospermum scoparium and L. ericoides (Angiospermae: Myrtaceae). *Mauri ora,* **1,** 5-12.

Burrows, C.J. (1994) The seeds always know best. *New Zealand Journal of Botany,* **32,** 349-363.

Cadenasso, M.L. & Pickett, S.T.A. (2000) Linking Forest Edge Structure to Edge Function: Mediation of Herbivore Damage. *Journal of Ecology,* **88,** 31-44.

Callaway, R.M. & Walker, L.R. (1997) Competition and Facilitation: A Synthetic Approach to Interactions in Plant Communities. *Ecology,* **78,** 1958-1965.

Carlo, T.A. & Yang, S. Network models of frugivory and seed dispersal: Challenges and opportunities. *Acta Oecologica,* **37,** 619-624.

Carnell, R. (2012) lhs: Latin Hypercube Samples.

Carnevale, N.J. & Montagnini, F. (2002) Facilitating regeneration of secondary forests with the use of mixed and pure plantations of indigenous tree species. *Forest Ecology and Management,* **163,** 217-227.

Castro, J., Zamora, R., Hódar, J.A., Gómez, J.M. & Gómez‐Aparicio, L. (2004) Benefits of Using Shrubs as Nurse Plants for Reforestation in Mediterranean Mountains: A 4‐Year Study. *Restoration Ecology,* **12,** 352-358.

Caughley, G. (1977) *Analysis of vertebrate populations*. Wiley, New York.

Cavallero, L., Raffaele, E. & Aizen, M.A. (2013) Birds as mediators of passive restoration during early post-fire recovery. *Biological Conservation,* **158,** 342-350.

Chan, S., McCreight, R., Walstad, J. & Spies, T. (1986) Notes: Evaluating Forest Vegetative Cover with Computerized Analysis of Fisheye Photographs. *Forest Science,* **32,** 1085-1091.

Choi, Y.D. (2007) Restoration Ecology to the Future: A Call for New Paradigm. *Restoration Ecology,* **15,** 351-353.

Clapperton, B.K. (2006) *A review of the current knowledge of rodent behaviour in relation to control devices*. Science & Technical Pub., Department of Conservation.

Clarkson, B.R., Sorrell, B., Reeves, P., Champion, P., Partridge, T. & Clarkson, B.D. (2004) *Handbook for Monitoring Wetland Condition: Coordinated*

Monitoring for New Zealand Wetlands. Ministry for the Environment, Wellington

Clements, F.E. (1916) *Plant succession: an analysis of the development of vegetation*. Carnegie Institution of Washington.

Clout, M. (2001) Where protection is not enough: active conservation in New Zealand. *Trends in Ecology & Evolution,* **16,** 415-416.

Clout, M. & Hay, J. (1989) The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. *New Zealand Journal of Ecology,* **12,** 27-33.

Cole, R.J., Holl, K.D., Keene, C.L. & Zahawi, R.A. (2011) Direct seeding of late-successional trees to restore tropical montane forest. *Forest Ecology and Management,* **261,** 1590-1597.

Conner, M.C., Labisky, R.F. & Progulske, D.R. (1983) Scent-station indices as measures of population abundance for bobcats, raccoons, gray foxes, and opossums. *Wildlife Society Bulletin***,** 146-152.

Coomes, D.A., Allen, R.B., Forsyth, D.M. & Lee, W.G. (2003) Factors Preventing the Recovery of New Zealand Forests Following Control of Invasive Deer

Factores que Previenen la Recuperación de Bosques de Nueva Zelanda Después del Control del Venado Invasor. *Conservation Biology,* **17,** 450-459.

Corbin, J.D. & Holl, K.D. (2012) Applied nucleation as a forest restoration strategy. *Forest Ecology and Management,* **265,** 37-46.

Corlett, R. (2007) Pollination or seed dispersal: which should we worry about most? *Seed dispersal: theory and its application in a changing world* (eds A. Dennis, E. Schupp, R. Green & D. Westcott), pp. 523-544. CABI Publishing, Wallingford, UK.

Cowan, P., Chilvers, B., Efford, M. & McElrea, G. (1997) Effects of possum browsing on northern rata, Orongorongo Valley, Wellington, New Zealand. *Journal of the Royal Society of New Zealand,* **27,** 173-179.

Cramer, V.A. & Hobbs, R.J. (2002) Ecological consequences of altered hydrological regimes in fragmented ecosystems in southern Australia: Impacts and possible management responses. *Austral Ecology,* **27,** 546-564.

Cramer, V.A., Hobbs, R.J. & Standish, R.J. (2008) What's new about old fields? Land abandonment and ecosystem assembly. *Trends in Ecology & Evolution,* **23,** 104-112.

Cubina, A. & Aide, T.M. (2001) The Effect of Distance from Forest Edge on Seed Rain and Soil Seed Bank in a Tropical Pasture. *Biotropica,* **33,** 260-267.

Davis, M.A. & Slobodkin, L.B. (2004) The science and values of restoration ecology. *Restoration Ecology,* **12,** 1-3.

de la Peña-Domene, M., Martínez-Garza, C., Palmas-Pérez, S., Rivas-Alonso, E. & Howe, H.F. (2014) Roles of Birds and Bats in Early Tropical-Forest Restoration. *PLoS ONE,* **9,** e104656.

de Souza Gomes Guarino, E. & Scariot, A. (2014) Direct seeding of dry forest tree species in abandoned pastures: effects of grass canopy and seed burial on germination. *Ecological Research,* **29,** 473-482.

Department of the Environment Water Heritage and the Arts (2009) National Guidelines for Notifying Change in Ecological Character of Australian Ramsar Sites (Article 3.2). Australian Government Department of the Environment, Water, Heritage and the Arts, Canberra.

Diamond, J. (1987) Reflections on goals and on the relationship between theory and practice. *Restoration ecology: a synthetic approach to ecological research* (eds W.R. Jordan III & M.E. Gilpin), pp. 329-336. Cambridge University Press, Cambridge, United Kingdom.

Dobson, A. (1979) Vegetation. *Ecology of Kowhai Bush* (eds D.M. Hunt & B.J. Gill), pp. 11-15. Mauri Ora Special Publication.

DOC (2014) Department of Conservation annual report for the year ended 30 June 2014. (ed. D.o. Conservation).

Duncan, R.S. & Chapman, C.A. (1999) Seed Dispersal and Potential Forest Succession in Abandoned Agriculture in Tropical Africa. *Ecological Applications,* **9,** 998-1008.

Dymond, J.R., Ausseil, A.-G.E. & Overton, J.M. (2008) A landscape approach for estimating the conservation value of sites and site-based projects, with examples from New Zealand. *Ecological Economics,* **66,** 275-281.

Elith, J., Leathwick, J.R. & Hastie, T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology,* **77,** 802-813.

Engel, V.L. & Parrotta, J.A. (2001) An evaluation of direct seeding for reforestation of degraded lands in central São Paulo state, Brazil. *Forest Ecology and Management,* **152,** 169-181.

Enright, N. (1989) Heathland vegetation of the Spirits Bay area, far northern New Zealand. *New Zealand Journal of Ecology***,** 63-75.

Enright, N. & Cameron, E. (1988) The soil seed bank of a kauri (Agathis australis) forest remnant near Auckland, New Zealand. *New Zealand Journal of Botany,* **26,** 223-236.

Esler, A.E. (1967) The vegetation of Kapiti Island. *New Zealand Journal of Botany,* **5,** 353-393.

Esler, A.E. & Astridge, S.J. (1974) Tea tree (Leptospermum) communities of the Waitakere Range, Auckland, New Zealand. *New Zealand Journal of Botany,* **12,** 485-501.

Ewers, R.M., Kliskey, A.D., Walker, S., Rutledge, D., Harding, J.S. & Didham, R.K. (2006) Past and future trajectories of forest loss in New Zealand. *Biological Conservation,* **133,** 312-325.

Fattorini, M. & Halle, S. (2004) The dynamic environmental filter model: how do filtering effects change in assembling communities after disturbance. *Assembly rules and restoration ecology: bridging the gap between theory and practice* (eds V.M. Temperton, R.J. Hobbs, T. Nuttle & S. Halle), pp. 96-114.

Finegan, B. & Delgado, D. (2000) Structural and Floristic Heterogeneity in a 30‐Year‐Old Costa Rican Rain Forest Restored on Pasture Through Natural Secondary Succession. *Restoration Ecology,* **8,** 380-393.

Forman, R.T. (1983) An ecology of the landscape. *BioScience,* **33,** 5351.

Forsyth, D.M., Link, W.A., Webster, R., Nugent, G. & Warburton, B. (2005) Nonlinearity and Seasonal Bias in an Index of Brushtail Possum Abundance. *The Journal of Wildlife Management,* **69,** 976-984.

Franks, S.J. (2003) Facilitation in multiple life-history stages: evidence for nucleated succession in coastal dunes. *Plant Ecology,* **168,** 1-11.

Frazer, G.W., Canham, C. & Lertzman, K. (1999) Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual

and program documentation. *Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York,* **36**.
Friedman, J.H. (2001) Greedy function approximation: a gradient boosting machine. *Annals of statistics***,** 1189-1232.
García, D. & Obeso, J.R. (2003) Facilitation by herbivore-mediated nurse plants in a threatened tree, Taxus baccata: local effects and landscape level consistency. *Ecography,* **26,** 739-750.
Gaston, K.J. (1996) Species-range-size distributions: patterns, mechanisms and implications. *Trends in Ecology & Evolution,* **11,** 197-201.
Ghazoul, J., Burivalova, Z., Garcia-Ulloa, J. & King, L.A. (2015) Conceptualizing Forest Degradation. *Trends in Ecology & Evolution,* **30,** 622-632.
Gibson, C. & Brown, V. (1991) The nature and rate of development of calcareous grassland in southern Britain. *Biological Conservation,* **58,** 297-316.
Gillies, C.A. & Williams, D. (2013) DOC tracking tunnel guide v2.5.2: Using tracking tunnels to monitor rodents and mustelids. Science & Capability Group, Department of Conservation Hamilton, New Zealand.
Goldberg, D.E. & Barton, A.M. (1992) Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *American naturalist***,** 771-801.
Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J. & Baraza, E. (2004) Applying Plant Facilitation to Forest Restoration: A Meta-Analysis of the Use of Shrubs as Nurse Plants. *Ecological Applications,* **14,** 1128-1138.
Graham, L.L.B. & Page, S.E. (2011) Artificial Bird Perches for the Regeneration of Degraded Tropical Peat Swamp Forest: A Restoration Tool with Limited Potential. *Restoration Ecology*. Blackwell Publishing Ltd.
Graham, L.L.B. & Page, S.E. (2012) Artificial Bird Perches for the Regeneration of Degraded Tropical Peat Swamp Forest: A Restoration Tool with Limited Potential. *Restoration Ecology,* **20,** 631-637.
Grant, D.A. (1967) Factors affecting the establishment of manuka (Leptospermum scoparium). *Proceedings of the NZ Weed and Pest Control Conference,* **20,** 129-134.
Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J. & Railsback, S.F. (2010) The ODD protocol: a review and first update. *Ecological modelling,* **221,** 2760-2768.
Grubb, P.J. (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological reviews of the Cambridge Philosophical Society,* **52,** 107-145.
Guevara, S. & Laborde, J. (1993) Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. *Frugivory and seed dispersal: ecological and evolutionary aspects*, pp. 319-338. Springer.
Hall, G. & McGlone, M. (2001) Forest reconstruction and past climatic estimates for a deforested region of south-eastern New Zealand. *Landscape Ecology,* **16,** 501-521.
Hall, G.M.J. & Hollinger, D.Y. (2000) Simulating New Zealand Forest Dynamics with a Generalized Temperate Forest Gap Model. *Ecological Applications,* **10,** 115-130.

Halle, S. (2007) Science, art, or application - The "Karma" of restoration ecology. *Restoration Ecology,* **15,** 358-361.
Hanski, I. & Ovaskainen, O. (2002) Extinction debt at extinction threshold. *Conservation Biology,* **16,** 666-673.
Herron, H., Clemens, J. & Greer, D.H. (2000) Contrasting seed germination responses to red and far-red light in *Leptospermum scoparium* and *Melicytus ramiflorus*. *Australian journal of plant physiology,* **27,** 1069-1076.
Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J., & (2013) dismo: Species distribution modeling.
Hill, R., Gourlay, A. & Barker, R. (2001) Survival of Ulex europaeus seeds in the soil at three sites in New Zealand. *New Zealand Journal of Botany,* **39,** 235-244.
Hobbs, R.J. & Cramer, V.A. (2008) Restoration Ecology: Interventionist Approaches for Restoring and Maintaining Ecosystem Function in the Face of Rapid Environmental Change. *Annual Review of Environment and Resources,* **33,** 39-61.
Hobbs, R.J., Cramer, V.A. & Kristjanson, L.J. (2003) What happens if we cannot fix it? Triage, palliative care and setting priorities in salinising landscapes. *Australian journal of botany,* **51,** 647-653.
Hobbs, R.J., Hallett, L.M., Ehrlich, P.R. & Mooney, H.A. (2011) Intervention Ecology: Applying Ecological Science in the Twenty-first Century. *BioScience,* **61,** 442-450.
Hobbs, R.J., Higgs, E. & Harris, J.A. (2009) Novel ecosystems: implications for conservation and restoration. *Trends in Ecology & Evolution,* **24,** 599-605.
Hobbs, R.J. & Norton, D.A. (1996) Towards a conceptual framework for restoration ecology. *Restoration Ecology,* **4,** 93.
Hobbs, R.J. & Norton, D.A. (2004) Ecological filters, thresholds, and gradients in resistance to ecosystem reassembly. *Assembly rules and restoration ecology: bridging the gap between theory and practice* (eds V.M. Temperton, R.J. Hobbs, T. Nuttle & S. Halle), pp. 72-95. Island Press, Washington D.C.
Holdaway, R.N., Worthy, T.H. & Tennyson, A.J. (2001) A working list of breeding bird species of the New Zealand region at first human contact. *New Zealand Journal of Zoology,* **28,** 119-187.
Holl, K.D. (1998) Do Bird Perching Structures Elevate Seed Rain and Seedling Establishment in Abandoned Tropical Pasture? *Restoration Ecology,* **6,** 253-261.
Holl, K.D. (1999) Factors Limiting Tropical Rain Forest Regeneration in Abandoned Pasture: Seed Rain, Seed Germination, Microclimate, and Soil. *Biotropica,* **31,** 229-242.
Holl, K.D. & Aide, T.M. (2011) When and where to actively restore ecosystems? *Forest Ecology and Management,* **261,** 1558-1563.
Holl, K.D., Loik, M.E., Lin, E.H.V. & Samuels, I.A. (2000) Tropical Montane Forest Restoration in Costa Rica: Overcoming Barriers to Dispersal and Establishment. *Restoration Ecology,* **8,** 339-349.
Holmgren, M. (2002) Exotic Herbivores as Drivers of Plant Invasion and Switch to Ecosystem Alternative States. *Biological Invasions,* **4,** 25-33.

Holmgren, M., Scheffer, M. & Huston, M.A. (1997) The Interplay of Facilitation and Competition in Plant Communities. *Ecology,* **78,** 1966-1975.
Hooper, E., Legendre, P. & Condit, R. (2005) Barriers to Forest Regeneration of Deforested and Abandoned Land in Panama. *Journal of Applied Ecology,* **42,** 1165-1174.
Howald, G., Donlan, C., Galván, J.P., Russell, J.C., Parkes, J., Samaniego, A., Wang, Y., Veitch, D., Genovesi, P. & Pascal, M. (2007) Invasive rodent eradication on islands. *Conservation Biology,* **21,** 1258-1268.
Howe, H.F. & Miriti, M.N. (2004) When Seed Dispersal Matters. *BioScience,* **54,** 651-660.
Howe, H.F. & Smallwood, J. (1982) Ecology of Seed Dispersal. *Annual Review of Ecology and Systematics,* **13,** 201-228.
Howell, C.J., Kelly, D. & Turnbull, M.H. (2002) Moa Ghosts Exorcised? New Zealand's Divaricate Shrubs Avoid Photoinhibition. *Functional Ecology,* **16,** 232-240.
Hutchings, S.A., Hancox, N. & Livingstone, P.G. (2013) A Strategic Approach to Eradication of Bovine TB from Wildlife in New Zealand. *Transboundary and Emerging Diseases,* **60,** 85-91.
Hutchinson, G.E. (1978) An introduction to population ecology.
Innes, J. (2001) Advances in New Zealand mammalogy 1990–2000: European rats. *Journal of the Royal Society of New Zealand,* **31,** 111-125.
Innes, J., Kelly, D., Overton, J.M. & Gillies, C. (2010) Predation and other factors currently limiting New Zealand forest birds. *New Zealand Journal of Ecology,* **34,** 86-114.
Innes, J., Warburton, B., Williams, D., Speed, H. & Bradfield, P. (1995) Large-scale poisoning of ship rats (*Rattus rattus*) in indigenous forests of the North Island, New Zealand. *New Zealand Journal of Ecology,* **19,** 5-17.
Jackson, S.T. & Overpeck, J.T. (2000) Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology,* **26,** 194-220.
Jacques, P. (2009) Awarua/Waituna Animal Pest Monitoring - Report May 2008 to June 2009. pp. 27. Department of Conservation
Jane, G. & Pracy, L. (1974a) Observations on two animal exclosures in Haurangi Forest over a period of 20 years. *New Zealand Journal of Forestry,* **1,** 103-113.
Jane, G. & Pracy, L.T. (1974b) Observations on two animal exclosures in Haurangi Forest over a period of twenty years (1951-1971). *New Zealand Journal of Forestry*.
Janzen, D. (2002) Tropical dry forest: area de conservacion Guanacaste, northwestern Costa Rica. *Handbook of ecological restoration* (eds M.R. Perrow & A.J. Davy), pp. 559-583. Cambridge University Press, Cambridge, UK.
Janzen, D.H. (1971) Seed Predation by Animals. *Annual Review of Ecology and Systematics,* **2,** 465-492.
Johnson, P. & Gerbeaux, P. (2004) *Wetland types in New Zealand*. Department of Conservation.
Johnson, P.N. (2001) Vegetation recovery after fire on a southern New Zealand peatland. *New Zealand Journal of Botany,* **39,** 251-267.

Kavermann, A.M., Paterson, M.J. & Ross, J.G. (2013) Sensitivity of audio-lured versus silent chew-track-cards and WaxTags to the presence of brushtail possums (*Trichosurus vulpecula*). *New Zealand Natural Sciences,* **38,** 1-8.

Kelly, D., Ladley, J.J. & Robertson, A.W. (2004) Is dispersal easier than pollination? Two tests in New Zealand Loranthaceae. *New Zealand Journal of Botany,* **42,** 89-103.

Kelly, D., Ladley, J.J., Robertson, A.W., Anderson, S.H., Wotton, D.M. & Wiser, S.K. (2010) Mutualisms with the wreckage of an avifauna: the status of bird pollination and fruit-dispersal in New Zealand. *New Zealand Journal of Ecology,* **34,** 66-66-85.

Kelm, D.H., Wiesner, K.R. & Helversen, O.v. (2008) Effects of Artificial Roosts for Frugivorous Bats on Seed Dispersal in a Neotropical Forest Pasture Mosaic

Efectos de Refugios Artificiales para Murciélagos Frugívoros sobre la Dispersión de Semillas en un Mosaico Bosque-Pastura Neotropical. *Conservation Biology,* **22,** 733-741.

Kitzberger, T., Aráoz, E., Gowda, J.H., Mermoz, M. & Morales, J.M. (2012) Decreases in fire spread probability with forest age promotes alternative community states, reduced resilience to climate variability and large fire regime shifts. *Ecosystems,* **15,** 97-112.

La Voie, C., Zimmermann, C. & Pellerin, S. (2001) Peatland restoration in southern Québec (Canada): a paleoecological perspective. *Écoscience***,** 247-258.

Ledgard, G. (2013) Land Use Change in the Southland Region. *Environment Southland Technical Report*, pp. 79 p.

Lee, W.G., Wilson, J.B. & Johnson, P.N. (1988) Fruit colour in relation to the ecology and habit of Coprosma (Rubiaceae) species in New Zealand. *Oikos***,** 325-331.

Lester, S.E., Ruttenberg, B.I., Gaines, S.D. & Kinlan, B.P. (2007) The relationship between dispersal ability and geographic range size. *Ecology Letters,* **10,** 745-758.

MacMahon, J.A. (1987) Disturbed lands and ecological theory: an essay about a mutualistic association. *Restoration ecology: a synthetic approach to ecological research* (eds W.R. Jordan III, M.E. Gilpin & J.D. Aber), pp. 221-237. Cambridge University Press, Cambridge, England.

Mark, A.F. & McLennan, B. (2005) The conservation status of New Zealand's indigenous grasslands. *New Zealand Journal of Botany,* **43,** 245-270.

Markl, J.S., Schleuning, M., Forget, P.M., Jordano, P., Lambert, J.E., Traveset, A., Wright, S.J. & Böhning-Gaese, K. (2012) Meta-Analysis of the Effects of Human Disturbance on Seed Dispersal by Animals. *Conservation Biology,* **26,** 1072-1081.

McClanahan, T. & Wolfe, R. (1987) Dispersal of ornithochorous seeds from forest edges in central Florida. *Vegetatio,* **71,** 107-112.

McClanahan, T.R. & Wolfe, R.W. (1993) Accelerating Forest Succession in a Fragmented Landscape: The Role of Birds and Perches. *Conservation Biology,* **7,** 279-288.

McDonnell, M.J. (1986) Old field vegetation height and the dispersal pattern of bird-disseminated woody plants. *Bulletin of the Torrey Botanical Club***,** 6-11.

McDonnell, M.J. & Stiles, E.W. (1983) The Structural Complexity of Old Field Vegetation and the Recruitment of Bird-Dispersed Plant Species. *Oecologia,* **56,** 109-116.
McGlone, M. (1983) Polynesian deforestation of New Zealand: a preliminary synthesis. *Archaeology in Oceania***,** 11-25.
McGlone, M. (1989) The Polynesian settlement of New Zealand in relation to environmental and biotic changes. *New Zealand Journal of Ecology***,** 115-129.
McGlone, M.S. (2001) The origin of the indigenous grasslands of southeastern South Island in relation to pre-human woody ecosystems. *New Zealand Journal of Ecology***,** 1-15.
McGlone, M.S. (2009) Postglacial history of New Zealand wetlands and implications for their conservation. *New Zealand Journal of Ecology,* **33,** 1-23.
McQueen, J. & Forester, L. (2000) Succession in the Kaimaumau gumland, Northland, New Zealand, following fire. Department of Conservation Wellington, New Zealand.
McWethy, D.B., Whitlock, C., Wilmshurst, J.M., McGlone, M.S., Fromont, M., Li, X., Dieffenbacher-Krall, A., Hobbs, W.O., Fritz, S.C. & Cook, E.R. (2010) Rapid landscape transformation in South Island, New Zealand, following initial Polynesian settlement. *Proceedings of the National Academy of Sciences,* **107,** 21343-21348.
Melo, F.P.L., Pinto, S.R.R., Brancalion, P.H.S., Castro, P.S., Rodrigues, R.R., Aronson, J. & Tabarelli, M. (2013) Priority setting for scaling-up tropical forest restoration projects: Early lessons from the Atlantic Forest Restoration Pact. *Environmental Science & Policy,* **33,** 395-404.
Messaoud, Y. & Houle, G. (2006) Spatial Patterns of Tree Seedling Establishment and Their Relationship to Environmental Variables in a Cold-Temperate Deciduous Forest of Eastern North America. *Plant Ecology,* **185,** 319-331.
Meurk, C.D. & Hall, G.M. (2006) Options for enhancing forest biodiversity across New Zealand's managed landscapes based on ecosystem modelling and spatial design. *New Zealand Journal of Ecology***,** 131-146.
Mladenoff, D.J. & Baker, W.L. (1999) Development of forest and landscape modeling approaches. *Spatial modeling of forest landscape change: approaches and applications***,** 1-13.
Moles, A.T. & Drake, D.R. (1999) Post‐dispersal seed predation on eleven large‐seeded species from the New Zealand flora: A preliminary study in secondary forest. *New Zealand Journal of Botany,* **37,** 679-685.
Molloy, B.P.J., Burrows, C.J., Cox, J.E., Johnston, J.A. & Wardle, P. (1963) Distribution of subfossil forest remains, eastern South Island, New Zealand. *New Zealand Journal of Botany,* **1,** 68-77.
Moors, P.J., Atkinson, I.A.E. & Sherley, G.H. (1992) Reducing the rat threat to island birds. *Bird Conservation International,* **2,** 93-114.
Moran, C., Catterall, C.P. & Kanowski, J. (2009) Reduced dispersal of native plant species as a consequence of the reduced abundance of frugivore species in fragmented rainforest. *Biological Conservation,* **142,** 541-552.
Moss, G. (1959) The gorse seed problem. *Proc. 12th NZ Weed and Pest Control Conference*, pp. 59-63.

Muller, C.H. (1969) Allelopathy as a Factor in Ecological Process. *Vegetatio,* **18,** 348-357.
Myster, R. (2004) Regeneration filters in post-agricultural fields of Puerto Rico and Ecuador. *Plant Ecology,* **172,** 199-209.
Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution,* **4,** 133-142.
Nepstad, D.C., Uhl, C., Pereira, C.A. & Silva, J.M.C.d. (1996) A Comparative Study of Tree Establishment in Abandoned Pasture and Mature Forest of Eastern Amazonia. *Oikos,* **76,** 25-39.
North, S.G., Bullock, D.J. & Dulloo, M.E. (1994) Changes in the vegetation and reptile populations on Round Island, Mauritius, following eradication of rabbits. *Biological Conservation,* **67,** 21-28.
Norton, D.A. (2009) Species Invasions and the Limits to Restoration: Learning from the New Zealand Experience. *Science,* **325,** 569-571.
Norvell, R.E., Howe, F.P. & Parrish, J.R. (2003) A Seven-Year Comparison of Relative-Abundance and Distance-Sampling Methods. *The Auk,* **120,** 1013-1028.
NPCA (2010) Possum population monitoring using the Waxtag® method. pp. 44. National Possum Control Agencies, Wellington, New Zealand.
NPCA (2011) Possum population monitoring using the trap catch method. pp. 44. National Possum Control Agencies, Wellington, New Zealand.
Nugent, G., Fraser, W. & Sweetapple, P. (2001) Top down or bottom up? Comparing the impacts of introduced arboreal possums and 'terrestrial' ruminants on native forests in New Zealand. *Biological Conservation,* **99,** 65-79.
Nugent, G., Morgan, D., Clayton, R. & Warburton, B. (2010) Improving the efficacy of aerial poisoning of brushtail possums (*Trichosurus vulpecula*) through reduced fragmentation of bait. *International Journal of Pest Management,* **57,** 51-59.
Nugent, G., Sweetapple, P.J., Coleman, J.D. & Suisted, P. (2000) Possum feeding patterns; dietary tactics of a somewhat folivore. *The brushtail possum: biology, impact and management of an introduced marsupial.* (ed. T.L. Montague), pp. 10-23. Manaaki Whenua Press, Lincoln, New Zealand.
Nugent, G., Warburton, B., Thomson, C., Cross, M.L. & Coleman, M.C. (2012) Bait aggregation to reduce cost and toxin use in aerial 1080 baiting of small mammal pests in New Zealand. *Pest Management Science,* **68,** 1374-1379.
O'Sullivan, D. & Perry, G.L. (2013) *Spatial simulation: exploring pattern and process*. John Wiley & Sons.
Odion, D.C., Moritz, M.A. & DellaSala, D.A. (2010) Alternative community states maintained by fire in the Klamath Mountains, USA. *Journal of Ecology,* **98,** 96-105.
Ogden, J., Basher, L. & McGlone, M. (1998) Fire, forest regeneration and links with early human habitation: evidence from New Zealand. *Annals of Botany***,** 687-696.
Ogden, J. & Stewart, G.H. (1995) Community dynamics of the New Zealand conifers. *Ecology of the southern conifers***,** 81-119.

Ogilvie, S.C., Paterson, A.M., Ross, J.G. & Thomas, M.D. (2006) Improving techniques for the WaxTag® possum (*Trichosurus vulpecula*) monitoring index. *New Zealand Plant Protection,* **59,** 28.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2013) vegan: Community Ecology Package. R
package version 2.0-10.

Parrotta, J.A. (1992) The role of plantation forests in rehabilitating degraded tropical ecosystems. *Agriculture, Ecosystems & Environment,* **41,** 115-133.

Partridge, T. (1989) Soil seed banks of secondary vegetation on the Port Hills and Banks Peninsula, Canterbury, New Zealand, and their role in succession. *New Zealand Journal of Botany,* **27,** 421-435.

Pendleton, G.W. (1995) Effects of sampling strategy, detection probability, and independence of counts on the use of point counts. *Monitoring Bird Populations by Point Counts, US Department of Agriculture, Forest Service general technical report, PSW-GTR-149***,** 131-133.

Peres-Neto, P.R., Legendre, P., Dray, S. & Borcard, D. (2006) Variation Partitioning of Species Data Matrices: Estimation and Comparison of Fractions. *Ecology,* **87,** 2614-2625.

Perry, G.L. & Enright, N.J. (2002) Humans, fire and landscape pattern: understanding a maquis‐forest complex, Mont Do, New Caledonia, using a spatial 'state‐and‐transition' model. *Journal of Biogeography,* **29,** 1143-1158.

Perry, G.L., Ogden, J., Enright, N.J. & Davy, L.V. (2010) Vegetation patterns and trajectories in disturbed landscapes, Great Barrier Island, northern New Zealand. *New Zealand Journal of Ecology***,** 311-323.

Perry, G.L., Wilmshurst, J.M., McGlone, M.S., McWethy, D.B. & Whitlock, C. (2012) Explaining fire‐driven landscape transformation during the Initial Burning Period of New Zealand's prehistory. *Global Change Biology,* **18,** 1609-1621.

Perry, G.L.W. & Enright, N.J. (2006) Spatial modelling of vegetation change in dynamic landscapes: a review of methods and applications. *Progress in Physical Geography,* **30,** 47-72.

Perry, G.L.W. & Millington, J.D.A. (2008) Spatial modelling of succession-disturbance dynamics in forest ecosystems: Concepts and examples. *Perspectives in Plant Ecology, Evolution and Systematics,* **9,** 191-210.

Perry, G.L.W., Wilmshurst, J.M. & McGlone, M.S. (2014) Ecology and long-term history of fire in New Zealand. *New Zealand Journal of Ecology,* **38,** 157-176.

Perry, G.W., Wilmshurst, J., Ogden, J. & Enright, N. (2015) Exotic Mammals and Invasive Plants Alter Fire-Related Thresholds in Southern Temperate Forested Landscapes. *Ecosystems***,** 1-16.

Petraitis, P.S. & Latham, R.E. (1999) The importance of scale in testing the origins of alternative community states. *Ecology,* **80,** 429-442.

Pickerell, G.A., O'Donnell, C.F.J., Wilson, D.J. & Seddon, P.J. (2014) How can we detect introduced mammalian predators in non-forest habitats? A comparison of techniques. *New Zealand Journal of Ecology,* **38,** 86-102.

Pollock, K.H., Nichols, J.D., Simons, T.R., Farnsworth, G.L., Bailey, L.L. & Sauer, J.R. (2002) Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics,* **13,** 105-119.

Powlesland, R.G., Moran, L.R. & Wotton, D.M. (2011) Satellite tracking of kereru (Hemiphaga novaeseelandiae) in Southland, New Zealand: impacts, movements and home range. *New Zealand Journal of Ecology,* **35,** 229.

Pulliam, H.R. (2000) On the relationship between niche and distribution. *Ecology Letters,* **3,** 349-361.

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramsey, D., Efford, M., Ball, S. & Nugent, G. (2005) The evaluation of indices of animal abundance using spatial simulation of animal trapping. *Wildlife Research,* **32,** 229-237.

Reid, J.L., Holl, K.D. & Zahawi, R.A. (2014) Seed dispersal limitations shift over time in tropical forest restoration. *Ecological Applications*.

Reynolds, H.L., Packer, A., Bever, J.D. & Clay, K. (2003) Grassroots Ecology: Plant-Microbe-Soil Interactions as Drivers of Plant Community Structure and Dynamics. *Ecology,* **84,** 2281-2291.

Richardson, S.J., Holdaway, R.J. & Carswell, F.E. (2014) Evidence for arrested successional processes after fire in the Waikare River catchment, Te Urewera. *New Zealand Journal of Ecology***,** 221-229.

Robertson, H.A. (2016) Wetland reserves in New Zealand: the status of protected areas between 1990 and 2013. *New Zealand Journal of Ecology,* **40,** 0-0.

Robertson, H.A. & Suggate, R. (2011) Arawai Kākāriki Wetland Restoration Programme 2007-2010: Implementation Report. Research and Development Group, Department of Conservation.

Rodrigues, R.R., Lima, R.A.F., Gandolfi, S. & Nave, A.G. (2009) On the restoration of high diversity forests: 30 years of experience in the Brazilian Atlantic Forest. *Biological Conservation,* **142,** 1242-1251.

Rodríguez, J.P. & Rodríguez-Clark, K.M. (2001) Even 'paper parks' are important. *Trends in Ecology & Evolution,* **16,** 17.

Rogers, G.M. & Leathwick, J.R. (1994) North Island serai tussock grasslands: 2. Autogenic succession: Change of tussock grassland to Shrubland. *New Zealand Journal of Botany,* **32,** 287-303.

Rose, A., Platt, K. & Frampton, C. (1995) Vegetation change over 25 years in a New Zealand short-tussock grassland: effects of sheep grazing and exotic invasions. *New Zealand Journal of Ecology***,** 163-174.

Rouco, C., Norbury, G.L., Smith, J., Byrom, A.E. & Pech, R.P. (2013) Population density estimates of brushtail possums (*Trichosurus vulpecul*a) in dry grassland in New Zealand. *New Zealand Journal of Ecology,* **37,** 12-17.

Roy, V., Ruel, J.-C. & Plamondon, A.P. (2000) Establishment, growth and survival of natural regeneration after clearcutting and drainage on forested wetlands. *Forest Ecology and Management,* **129,** 253-267.

Ruffell, J., Innes, J. & Didham, R.K. (2015) Efficacy of chew-track-card indices of rat and possum abundance across widely varying pest densities. *New Zealand Journal of Ecology,* **39,** 0-0.

Ruiz-Jaen, M.C. & Mitchell Aide, T. (2005) Restoration Success: How Is It Being Measured? *Restoration Ecology,* **13,** 569-577.

Ruscoe, W.A., Goldsmith, R. & Choquenot, D. (2001) A comparison of population estimates and abundance indices for house mice inhabiting beech forests in New Zealand. *Wildlife Research,* **28,** 173-178.

Salmon, J. (1975) The influence of man on the biota. *Biogeography and Ecology in New Zealand* (ed. G. Kuschel), pp. 643-661. Junk, The Hague.

Schadewinkel, R.B., Senior, A.M., Wilson, D.J. & Jamieson, I.G. (2014) Effects on South Island robins (*Petroica australis*) from pest control using aerially applied 1080 poison. *New Zealand Journal of Ecology,* **38,** 0-0.

Scheller, R.M., Domingo, J.B., Sturtevant, B.R., Williams, J.S., Rudy, A., Gustafson, E.J. & Mladenoff, D.J. (2007) Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. *Ecological modelling,* **201,** 409-419.

Schröder, A., Persson, L., de Roos, A.M. & Lundbery, P. (2005) Direct Experimental Evidence for Alternative Stable States: A Review. *Oikos,* **110,** 3-19.

Şekercioğlu, Ç.H., Daily, G.C. & Ehrlich, P.R. (2004) Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences,* **101,** 18042-18047.

SER [Society for Ecological Restoration International Science & Policy Working Group] (2004) The SER International Primer on Ecological Restoration

(available from http//http://www.ser.org) Society for Ecological Restoration International, Tuscon, Arizona.

Sharma, A., Jose, S., Bohn, K.K. & Andreu, M.G. (2012) Effects of reproduction methods and overstory species composition on understory light availability in longleaf pine–slash pine ecosystems. *Forest Ecology and Management,* **284,** 23-33.

Shiels, A.B. & Walker, L.R. (2003) Bird Perches Increase Forest Seeds on Puerto Rican Landslides. *Restoration Ecology,* **11,** 457-465.

Skalski, J.R. & Robson, D.S. (1992) *Techniques in Wildlife Investigations: Design and Analysis of Capture Data*. Academic Press.

Skaug, H., Fournier, D., Bolker, B., Magnusson, A. & Nielsen, A. (2014) Generalized Linear Mixed Models using AD Model Builder.

Slocum, M.G. (2001) How Tree Species Differ as Recruitment Foci in a Tropical Pasture. *Ecology,* **82,** 2547-2559.

Smale, M., Hall, G. & Gardner, R. (1995) Dynamics of kanuka (Kunzea ericoides) forest on South Kaipara spit, New Zealand, and the impact of fallow deer (Dama dama). *New Zealand Journal of Ecology,* **19,** 131-141.

Southland Regional Fire Authority (2015) Awarua fire records.

Standish, R.J., Cramer, V.A., Wild, S.L. & Hobbs, R.J. (2007) Seed dispersal and recruitment limitation are barriers to native recolonization of old-fields in western Australia. *Journal of Applied Ecology,* **44,** 435-445.

Stephens, J., Molan, P.C. & Clarkson, B.D. (2005) A review of Leptospermum scoparium (Myrtaceae) in New Zealand. *New Zealand Journal of Botany,* **43,** 431-449.

Steven, D.D. (1991a) Experiments on Mechanisms of Tree Establishment in Old-Field Succession: Seedling Emergence. *Ecology,* **72,** 1066-1075.

Steven, D.D. (1991b) Experiments on Mechanisms of Tree Establishment in Old-Field Succession: Seedling Survival and Growth. *Ecology,* **72,** 1076-1088.

Stewart, G.H. & Burrows, L.E. (1989) The impact of white-tailed deer Odocoileus virginianus on regeneration in the coastal forests of Stewart Island, New Zealand. *Biological Conservation,* **49,** 275-293.

Suding, K.N., Gross, K.L. & Houseman, G.R. (2004a) Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution,* **19,** 46-53.

Suding, K.N. & Hobbs, R.J. (2009) Threshold models in restoration and conservation: a developing framework. *Trends in Ecology & Evolution,* **24,** 271-279.

Sullivan, J.J., Williams, P.J. & Timmins, S.M. (2007) Secondary forest succession differs through naturalised gorse and native kānuka near Wellington and Nelson. *New Zealand Journal of Ecology,* **31,** 22-38.

Sweeney, B.W., Czapka, S.J. & Yerkes, T. (2002) Riparian Forest Restoration: Increasing Success by Reducing Plant Competition and Herbivory. *Restoration Ecology,* **10,** 392-400.

Sweetapple, P. & Nugent, G. (2009) Possum demographics and distribution after reduction to near–zero density. *New Zealand Journal of Zoology,* **36,** 461-471.

Sweetapple, P. & Nugent, G. (2011) Chew-track-cards: a multiple-species small mammal detection device. *New Zealand Journal of Ecology,* **35,** 153.

Thiele, J.C., Kurth, W. & Grimm, V. (2012) RNetLogo: an R package for running and exploring individual‐based models implemented in NETLOGO. *Methods in Ecology and Evolution,* **3,** 480-483.

Thomas, B.W. & Taylor, R.H. (2002) A history of ground-based rodent eradication techniques developed in New Zealand, 1959–1993. *Turning the tide: the eradication of invasive species***,** 301-310.

Thomas, M., Brown, J., Maddigan, F. & Sessions, L. (2003) Comparison of trap-catch and bait interference methods for estimating possum densities. *New Zealand Plant Protection***,** 81-85.

Thomas, M.D. (1999) Feasibility of using wax-blocks to measure rodent and possum abundance and changes in population size. *Science for Conservation C,* **127,** 39-48.

Tilman, D. (1982) *Resource Competition and Community Structure.* Princeton University Press Princeton, NJ.

Towns, D.R. & Broome, K.G. (2003) From small Maria to massive Campbell: forty years of rat eradications from New Zealand islands. *New Zealand Journal of Zoology,* **30,** 377 - 398.

Treskonova, M. (1991) Changes in the structure of tall tussock grasslands and infestation by species of Hieracium in the Mackenzie Country, New Zealand. *New Zealand Journal of Ecology***,** 65-78.

Turnbull, L.A., Crawley, M.J. & Rees, M. (2000) Are Plant Populations Seed-Limited? A Review of Seed Sowing Experiments. *Oikos,* **88,** 225-238.

Turner, M.G., Gardner, R.H. & O'Neill, R.V. (2001) *Landscape ecology in theory and practice: pattern and process*. Springer Science & Business Media.

Uhl, C., Buschbacher, R. & Serrao, E.A.S. (1988) Abandoned Pastures in Eastern Amazonia. I. Patterns of Plant Succession. *Journal of Ecology,* **76,** 663-681.

Van Diggelen, R., Grootjans, A.P. & Harris, J.A. (2001) Ecological Restoration: State of the Art or State of the Science? *Restoration Ecology,* **9,** 115-118.

Vieira, D.L. & Scariot, A. (2006) Principles of natural regeneration of tropical dry forests for restoration. *Restoration Ecology,* **14,** 11-20.

Vitousek, P.M., D'antonio, C.M., Loope, L.L., Rejmanek, M. & Westbrooks, R. (1997) Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology***,** 1-16.

Wang, B.C. & Smith, T.B. (2002) Closing the seed dispersal loop. *Trends in Ecology & Evolution,* **17,** 379-386.

Wang, Y., Naumann, U., Wright, S. & Warton, D. (2014) mvabund: Statistical Methods for Analysing Multivariate Abundance Data.

Warburton, B., Barker, R. & Coleman, M. (2004) Evaluation of two relative-abundance indices to monitor brushtail possums in New Zealand. *Wildlife Research,* **31,** 397-401.

Wardle, D.A., Barker, G.M., Yeates, G.W., Bonner, K.I. & Ghani, A. (2001) Introduced Browsing Mammals in New Zealand Natural Forests: Aboveground and Belowground Consequences. *Ecological Monographs,* **71,** 587-614.

Wardle, P. (1991) *Vegetation of New Zealand*. CUP Archive.

Wearne, L.J. & Morgan, J.W. (2006) Shrub invasion into subalpine vegetation: implications for restoration of the native ecosystem. *Plant Ecology,* **183,** 361-376.

Webb, C.J., Sykes, W.R. & Garnock-Jones, P.J. (1988) *Flora of New Zealand*. DSIR, Botany Div.

Wenny, D.G. (2000) Seed Dispersal, Seed Predation, and Seedling Recruitment of a Neotropical Montane Tree. *Ecological Monographs,* **70,** 331-351.

Wijdeven, S.M.J. & Kuzee, M.E. (2000) Seed Availability as a Limiting Factor in Forest Recovery Processes in Costa Rica. *Restoration Ecology,* **8,** 414-424.

Wilensky, U. (1999) Netlogo. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL. http://ccl.northwestern.edu/netlogo/.

Willard, D.A. & Cronin, T.M. (2007) Paleoecology and ecosystem restoration: case studies from Chesapeake Bay and the Florida Everglades. *Frontiers in Ecology and the Environment,* **5,** 491-498.

Williams, P.A. & Karl, B.J. (2002) Birds and small mammals in kanuka (*Kunzea ericoides*) and gorse (*Ulex europaeus*) scrub and the resulting seed rain and seedling dynamics. *New Zealand Journal of Ecology,* **26,** 31-42.

Williams, P.A., Karl, B.J., Bannister, P. & Lee, W.G. (2000) Small mammals as potential seed dispersers in New Zealand. *Austral Ecology,* **25,** 523-532.

Wilmshurst, J.M. (1997) The impact of human settlement on vegetation and soil stability in Hawke's Bay, New Zealand. *New Zealand Journal of Botany,* **35,** 97-111.

Wilmshurst, J.M., Eden, D.N. & Froggatt, P.C. (1999) Late Holocene forest disturbance in Gisborne, New Zealand: a comparison of terrestrial and marine pollen records. *New Zealand Journal of Botany,* **37,** 523-540.

Wilson, D.J., Lee, W.G., Webster, R.A. & Allen, R.B. (2003) Effects of possums and rats on seedling establishment at two forest sites in New Zealand. *New Zealand Journal of Ecology,* **27,** 147-155.

Wilson, D.J., Ruscoe, W.A., Burrows, L.E., McElrea, L.M. & Choquenot, D. (2006) An experimental study of the impacts of understorey forest vegetation and herbivory by red deer and rodents on seedling establishment and species composition in Waitutu Forest, New Zealand. *New Zealand Journal of Ecology,* **30,** 191-207.

Wilson, H.D. (1994) Regeneration of native forest on Hinewai Reserve, Banks Peninsula. *New Zealand Journal of Botany,* **32,** 373-383.

Wilson, J.B. & Agnew, A.D. (1992) *Positive-feedback switches in plant communities*. Academic Press London.

Wiser, S.K., Bellingham, P.J. & Burrows, L.E. (2001) Managing biodiversity information: development of New Zealand's National Vegetation Survey databank. *New Zealand Journal of Ecology***,** 1-17.

Wotton, D.M. & Kelly, D. (2012) Do larger frugivores move seeds further? Body size, seed dispersal distance, and a case study of a large, sedentary pigeon. *Journal of Biogeography,* **39,** 1973-1983.

Wright, J. (2011) Evaluating the use of 1080: predators, poisons and silent forests. pp. 1-85. Parliamentary Commissioner for the Environment, Wellington, New Zealand.

Wunderle, J.M. (1997) The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecology and Management,* **99,** 223-235.

Young, T.P., Chase, J.M. & Huddleston, R.T. (2001) Community succession and assembly comparing, contrasting and combining paradigms in the context of ecological restoration. *Ecological restoration,* **19,** 5-18.

Zahawi, R.A., Reid, J.L. & Holl, K.D. (2014) Hidden Costs of Passive Restoration. *Restoration Ecology,* **22,** 284-287.

Zanini, L. & Ganade, G. (2005) Restoration of Araucaria Forest: The Role of Perches, Pioneer Vegetation, and Soil Fertility. *Restoration Ecology,* **13,** 507-514.

Deputy Vice-Chancellor's Office
Postgraduate Office

UNIVERSITY OF CANTERBURY
Te Whare Wānanga o Waitaha
CHRISTCHURCH NEW ZEALAND

Co-Authorship Form

This form is to accompany the submission of any thesis that contains research reported in co-authored work that has been published, accepted for publication, or submitted for publication. A copy of this form should be included for each co-authored work that is included in the thesis. Completed forms should be included at the front (after the thesis abstract) of each copy of the thesis submitted for examination and library deposit.

Please indicate the chapter/section/pages of this thesis that are extracted from co-authored work and provide details of the publication or submission from the extract comes:

Chapter 3 has been submitted to Austral Ecology and accepted for revie

Please detail the nature and extent (%) of contribution by the candidate:

Olivia Burge designed the experiment, conducted fieldwork, undertook all analysis, and wrote the first, second and final drafts. 95%

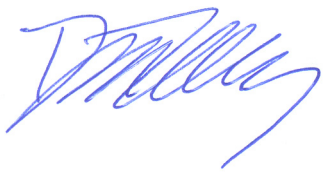
Prof Dave Kelly and Janet Wilmshurst (senior and associate supervisors, respectively) reviewed the first and second drafts. 2.5% each

Certification by Co-authors:

If there is more than one co-author then a single co-author can sign on behalf of all

The undersigned certifys that:

- The above statement correctly reflects the nature and extent of the PhD candidate's contribution to this co-authored work
- In cases where the candidate was the lead author of the co-authored work he or she wrote the text



Name: *Dave Kelly* Signature: Date:10 November, 2015